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Revision of Afrotropical *Udea* Guenée in Duponchel, 1845, with description of five new species of the *U. ferrugalis* (Hübner, 1796) group (Lepidoptera, Crambidae, Spilomelinae)

Richard Mally[1], Leif Aarvik[2], Timm Karisch[3], David C. Lees[4], Tobias Malm[5]

1 *Department of Forest Protection and Entomology, Czech University of Life Sciences, Prague, Kamýcká 129, 165 00 Prague 6 – Suchdol, Czech Republic; mally@fld.czu.cz*
2 *Natural History Museum, University of Oslo, Oslo, Norway; leif.aarvik@nhm.uio.no*
3 *Museum für Naturkunde und Vorgeschichte, Dessau, Germany; Timm.Karisch@naturkunde.dessau.de*
4 *Insects Division, Natural History Museum, Cromwell Road, SW7 5BD, London, UK; david.lees@nhm.ac.uk*
5 *Naturhistoriska Riksmuseet, Stockholm, Sweden; tobias.malm@nrm.se*

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Abstract. The *Udea* species (currently six) present in the Afrotropical realm are revised based on adults. *Phlyctaenia epicoena* Meyrick, 1937 **syn. nov.** is found to be identical with *U. ferrugalis* (Hübner, 1796). *Udea delineatalis* (Walker in Melliss 1875) and *U. hageni* Viette, 1952 are redescribed. In addition, five species of *Udea* are described as new to science: *U. kirinyaga* Mally **sp. nov.** from Mount Kenya in Kenya, *U. nicholsae* Mally **sp. nov.**, *U. meruensis* Mally **sp. nov.** and *U. momella* Mally **sp. nov.**, all three from Mount Meru in Tanzania, and *U. namaquana* Karisch & Mally **sp. nov.** from South Africa. A phylogenetic analysis based on morphological data and mitochondrial COI as well as the nuclear wingless gene, where available, places the new species in the *U. ferrugalis* species group, which also comprises *U. ferrugalis* as well as *U. delineatalis* from the oceanic island of St. Helena. Another island endemic, *Udea hageni* from Tristan da Cunha, is found to be a member of the *U. numeralis* group, as sister to *U. numeralis*. An additional synapomorphic character of the genitalia is recognised for the *U. ferrugalis* group. *Udea infuscalis* (Zeller, 1852) and *U. melanostictalis* (Hampson in Poulton 1916) are misplaced in *Udea* and transferred to Pyraustinae, as *Lirabotys infuscalis* **comb. nov.** and *Achyra melanostictalis* **comb. nov.**, respectively. Adults, tympanic organs, and genitalia of both sexes, where available, are illustrated. A checklist summarises the now eight Afrotropical *Udea* species.

Introduction

Udea Guenée in Duponchel 1845 is a genus of snout moths (Pyraloidea) in the diverse subfamily Spilomelinae, where it is placed in the tribe Udeini (Mally et al. 2019). It currently comprises 214 species worldwide (Nuss et al. 2003–2022). Species of *Udea* are present on all continents except Antarctica, with the highest diversity in the temperate regions of both hemispheres and on oceanic islands (Zimmerman 1958; Munroe 1966). For the Afrotropical region, there are currently six species known: the Central African *U. epicoena* (Meyrick, 1937), the widespread *U. ferrugalis* (Hübner, 1796), the South African *U. infuscalis* (Zeller, 1852), the East African *U. melanostictalis*

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(Hampson in Poulton 1916), and two endemic species on Atlantic islands: *U. delineatalis* (Walker in Meliss 1875) on St. Helena, and *U. hageni* Viette, 1952 on Tristan da Cunha (De Prins and De Prins 2011–2022; Nuss et al. 2003–2022). This is a low species number compared to other tropical regions: 49 species are known for the Neotropics, and 50 for the Austral-Asian region (Munroe 1995; Shaffer et al. 1996; Nuss et al. 2003–2022).

Here, we re-examine the *Udea* species of Sub-Saharan Africa, re-describe poorly known species, and describe new species from East African mountains and South Africa. Furthermore, we add morphological and DNA sequence data to the datasets of Mally and Nuss (2011) and Mally et al. (2016), and analyse the extended dataset in terms of phylogenetic relationships.

Methods

The material investigated in terms of morphology is stated in the "Material examined" sections of the respective species (see Taxonomy part of the results). The datasets of Mally and Nuss (2011) and Mally et al. (2016) were complemented by several additional species, which are summarised in Table 1. DNA lab procedures and morphological investigation and documentation follow Mally et al. (2016). Terminology of the wing pattern elements follows Nuss (2005), and mostly Kristensen (2003) for the genitalia; the term 'praephallus' is used for the posterior end of the phallus apodeme. The molecular work was conducted in the DNA lab of the Department of Biology, University of Bergen. For *U. infuscalis*, DNA Barcode sequences from 26 specimens were available in the BOLD (Barcode of Life Data Systems) database (Ratnasingham and Hebert 2007; https://v4.boldsystems.org/), and a strict consensus sequence from these sequences was used for phylogenetic analyses.

The genetic and morphological data of the new species were combined with the dataset of Mally et al. (2016), including the omitted character 17 from Mally and Nuss (2011), and extended by two more characters (characters 17 and 18, marked with [new] below), resulting in the following 26 coded morphological characters: 1) Fore wing – postmedial line: with loop (0), with rectangular or less angled bow (1); 2) Fore wing – colouration of discoidal stigmata: identical with ground colour of wing (0), darker than ground colour of wing (1); 3) Fore wing – apical dark spots at end of veins Sc and R1 – 4: absent (0), present (1); 4) Wings – intersexual size difference: wing length and shape of fore wing apex same in both sexes (0), in female wing length reduced in female, fore wing apex more pointed in female as compared to male (1); 5) Hind wing – intersexual colouration difference: equally dark in female and in male (0); darker in female than in male (1); 6) Cornuti in phallus: absent (0), present (1); 7) Number of cornuti: one or two (0), ≥ four (1) (condition with three cornuti was not observed); 8) Praephallus – sclerotised ridge: absent (0), present (1); 9) Praephallus – location and shape of sclerotised ridge: ventrally projecting tooth- to hook-shaped process (0), dextrally projecting short denticulate ridge (1); 10) Praephallus – sclerotised, granulated area: absent (0), present (1); 11) Praephallus – location of sclerotised, granulated area: most posteriorly (0), distad from posterior end (due to posteriad elongation of the praephallus) (1); 12) Vesica (endotheca) – cluster of small cornuti at posterior end of uneverted vesica (close to the junction of vesica and praephallus): absent (0), present (1); 13) Praephallus – ventrally with longitudinal, twined split: absent (0), present (1); 14) Opening of ductus ejaculatorius in the phallus: anterior (0), anterodorsal (1); 15) Juxta – median apical split: absent (0), present (1); 16) Fibula: absent (0), present (1); 17) [new] Orientation of fibula

base: towards distal sacculus end (0) (Fig. 23a), towards sacculus centre or base (1) (e.g. Fig. 24a); 18) [new] Maximum breadth of sacculus: distad of fibula base (0) (Fig. 23a), basad of or at fibula base (1) (e.g. Fig. 24a); 19) Uncus – apex with bulbous thickening: absent (0), present (1); 20) Posterior arm of signum: elongated towards a bodkin-shaped acute tip (0), convex sides, converging towards a rounded tip (1); 21) Transverse signum ridge: absent (0), present (1); 22) Accessory signum anterior of ductus bursae: absent (0), present (1); 23) Ductus bursae – projection at anterior end: absent (0), present (1); 24) Ductus bursae – projection at posterior end: absent (0), present (1); 25) Ductus bursae – length: as long as or longer than corpus bursae (0), conspicuously shorter than corpus bursae (1); 26) Ductus bursae – sclerotisation (excluding the

Table 1. Summary of species added to the phylogenetic dataset of Mally et al. (2016). Column 1 mentions the DNA voucher in brackets, if applicable; column 2 states the source for identifying the species; column 3 summarises the locality where the specimen was collected; columns 4 and 5 state the unique identifiers for *COI* and *wingless* sequences, respectively, with the respective GenSeq status according to Chakrabarty et al. (2013), the sequence database, and reference where the sequence was published in brackets.

Species (DNA voucher)	**Identification source**	**Sampling locality**	***COI* sequence identification number (GenSeq status; database; reference)**	***wingless* sequence identification number (GenSeq status; database; reference)**
Udea delineatalis (Walker in Melliss 1875)	Melliss (1875); Cotype	St. Helena	–	–
Udea donzelalis (Guenée, 1854) (ZMBN Lep090)	Mally et al. (2018)	France, Cantal	MG523938 (genseq-3; NCBI; Mally et al. 2018)	MG523985 (genseq-3; NCBI; Mally et al. 2018)
Udea hageni Viette, 1952	Viette (1952)	Tristan da Cunha	–	–
Udea kirinyaga Mally, sp. nov. (ZMBN Lep135)	this study	Kenya, Central Province, Mt. Kenya southern slope, Castle Forest Lodge	ON206730 (genseq-1; NCBI; this study)	ON206634 (genseq-1; NCBI; this study)
Udea meruensis Mally, sp. nov. (ZMBN Lep143)	this study	Tanzania, Arumeru District, Mt. Meru Forest Reserve	ON206731 (genseq-1; NCBI; this study)	–
Udea momella Mally, sp. nov.	this study	Tanzania, Arusha Region, Mount Meru, Arusha National Park, Momella	–	–
Udea namaquana Karisch & Mally, sp. nov.	this study	South Africa, Northern Cape, Namaqua district, Hondeklipbaai	–	–
Udea nicholsae Mally, sp. nov.	this study	Tanzania, Arusha Region, Mount Meru, Arusha National Park, Momella	–	–
Udea swezeyi (Zimmerman, 1951) (WPH051)	Zimmerman (1951)	Hawaii	JX017840 (genseq-4; NCBI; Haines and Rubinoff 2012)	JX018119 (genseq-4; NCBI; Haines and Rubinoff 2012)
Udeoides bonakandaiensis Maes, 2006 (ZMBN Lep144)	Maes (2006)	Malawi, Central Region, Lilongwe District, Ntchisi Forest Reserve	OP684786 (genseq-4; NCBI; this study)	OP715619 (genseq-4; NCBI; this study)
Achyra melanostictalis (Hampson in Poulton 1916), comb. nov.	Poulton (1916); Lecto- and Paralectotype	Somalia, Mandheera	–	–
Euclasta splendidalis (Herrich-Schäffer, 1848) (MTD Lep1466)	Popescu-Gorj and Constantinescu (1977)	Bulgaria, Black Sea coast near Kamchya	MK459751 (genseq-4; NCBI; Mally et al. 2019)	LR743194 (genseq-4; NCBI; Léger et al. 2020)
Lirabotys infuscalis (Zeller, 1852), comb. nov. (BC ZSM Lep 66598)	Zeller (1852); Holotype	South Africa, Gauteng, Mogale's Gate Biodiversity Centre	GWOTH807-12 (genseq-4; BOLD; this study)	–

Table 2. Morphomatrix of the investigated specimens; the characters are those used in the morphomatrix of Mally and Nuss (2011), plus the two newly added characters 17 and 18; newly investigated taxa are marked with an asterisk (*). Character numbers are vertical (01–26).

Taxa	Characters						Taxa	Characters					
	00000	00001	11111	11112	22222	2		00000	00001	11111	11112	22222	2
	12345	67890	12345	67890	12345	6		12345	67890	12345	67890	12345	6
*Euclasta splendidalis**	?1000	110?0	?1011	0??1?	10000	0	*Udea institalis*	00100	110?1	00101	10011	11000	1
*Lirabotys infuscalis**	11000	110?0	?1001	101??	?0000	0	*Udea itysalis*	?1100	110?0	?0001	10111	00100	1
*Achyra melanostictalis**	110??	?????	?????	????1	10001	0	*Udea kirinyaga**	?11??	100?0	?1010	1111?	?????	?
Deana hybreasalis	1?0?0	110?0	?0011	10110	00001	0	*Udea languidalis*	01100	110?1	10101	10011	11000	1
Mnesictena marmarina	0?1?0	110?0	?0010	10110	10001	1	*Udea liopis*	01100	100?0	?1010	0??10	00001	0
*Udeoides bonakandaiensis**	111??	110?0	?0010	1011?	?0000	1	*Udea lugubralis*	0110?	100?0	?1010	11110	10011	0
Udeoides muscosalis	101??	110?0	?0010	1011?	?0000	1	*Udea lutealis*	00100	110?1	00101	10011	11000	1
Udea accolalis	01000	100?0	?1010	11110	10011	0	*Udea maderensis*	01100	100?0	?1010	10110	10011	0
Udea alpinalis	??011	0?110	?0001	10011	01001	1	*Udea meruensis**	111??	100?0	?1010	1111?	?????	?
Udea austriacalis	0?010	0?0?0	?0001	10011	01001	1	*Udea momella**	111??	100?0	?1010	1?11?	?????	?
Udea azorensis	010??	100?0	?1011	11110	00011	1	*Udea murinalis*	01010	0?0?0	?0001	10011	01001	1
Udea bourgognealis	1?0?1	0?110	?0000	10011	01000	1	*Udea namaquana**	01100	100?0	?1010	11110	00011	0
Udea carniolica	01010	0?110	?0001	10011	01000	1	*Udea nebulalis*	01011	0?100	?0001	10011	01001	1
Udea costalis costalis	?1100	110?0	?0001	10111	00100	1	*Udea nicholsae**	111??	?????	?????	????0	00001	0
Udea costalis maurinalis	01100	110?0	?0001	10111	00100	1	*Udea nordmani*	01100	100?0	?1010	10110	00011	0
Udea decrepitalis	11100	0?0?0	?0101	10011	01001	0	*Udea numeralis*	01100	100?0	?0101	10011	01001	1
*Udea delineatalis**	01100	100?0	?1010	11110	10011	0	*Udea* cf. *numeralis*	01100	100?0	?0101	10011	01001	1
*Udea donzelalis**	01011	0?110	?0101	10011	01000	0	*Udea olivalis*	01100	110?1	00101	10011	11000	1
Udea ferrugalis	01000	100?0	?101?	11110	10011	0	*Udea prunalis*	01100	110?0	?0001	10011	11001	1
Udea fimbriatralis	01100	110?1	10101	10011	11000	1	*Udea pyranthes*	1100?	100?0	?1011	0??10	00001	0
Udea fulvalis	11100	110?1	00101	10011	11001	1	*Udea rhododendronalis*	??011	11110	?0001	10?11	01001	?
*Udea hageni**	?10??	10100	?0101	1001?	?????	?	*Udea rubigalis*	00100	100?0	?1011	11110	10011	1
Udea hamalis	11?00	0?0?0	?0001	10011	01001	0	*Udea ruckdescheli*	01100	110?0	?0101	10010	11000	0
Udea heterodoxa	110??	100?0	?1010	0??10	00001	0	*Udea swezeyi**	011??	100?0	?1011	0??10	00001	0
Udea inquinatalis	01100	0?0?0	?0001	10011	01001	0	*Udea uliginosalis*	??011	0?100	?0001	10011	01001	1

colliculum): completely membranous (0), partly sclerotised (1). The updated morphomatrix, including the species added in this study, is compiled in Table 2.

The genetic dataset comprised 1,822 nucleotides, consisting of 1,459 nucleotides of the mitochondrial *COI* (Cytochrome oxidase subunit I) gene including the "DNA Barcode" part, and 363 nucleotides of the nuclear *wingless* gene. For a number of species, no genetic data were available (see Table 1), and their phylogenetic placement was inferred based on the morphological data subset alone. Phylogenetic analysis was done using MrBayes 3.2.7a (Ronquist et al. 2012), and settings as well as data evaluation follow Mally et al. (2016). Analysis performance and effective sample sizes (ESS) were reviewed in Tracer 1.6 (Rambaut et al. 2014). The resulting phylogeny was illustrated with TreeGraph 2.15.0-887 beta (Stöver and Müller 2010) and edited for publishing with GIMP 2.10.32.

An elevation map of the southern Gregory Rift (Fig. 35) was generated with DIVA-GIS, version 7.5 (https://www.diva-gis.org) to illustrate the type localities of four of the newly described species. Shape files on country level elevation data were obtained from the DIVA-GIS website (https://www.diva-gis.org/gdata), and for African water bodies from RCMRD (http://geoportal.rcmrd.org/layers/servir%3Aafrica_water_bodies).

Repositories, institutional acronyms or institutional abbreviations

MNVD Museum für Naturkunde und Vorgeschichte Dessau, Germany;
NHMO Natural History Museum, University of Oslo, Norway;
NHMUK Natural History Museum London, United Kingdom;
NHRS Swedish Museum of Natural History Stockholm, Sweden;
OUMNH Oxford University Museum of Natural History, United Kingdom;
SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany;
SMTD Senckenberg Museum für Tierkunde Dresden, Germany;
ZMBN Zoological Museum, University of Bergen, Norway;
ZSM Zoologische Staatssammlungen München, Germany

Results

Morphology

Species of *Udea* share a number of common morphological features: ocelli present above distal edge of eyes, behind antennal base; chaetosemata absent; tibial spurs on fore-/mid-/hindlegs: 0/2/4; tympanal organs with fornix tympani protruding ventrad, venulae secundae absent.

Table 2 summarises the binary-coded morphological character states of the investigated *Udea* species and the outgroup taxa along with the data from Mally and Nuss (2011), which are complemented by the new morpho-characters 17 and 18.

Taxonomy

In the following, the known Afrotropical *Udea* species are redescribed in alphabetical order before describing newly discovered species, arranged geographically from North to South by their type localities. *Udea ferrugalis* is a well-characterised species (see e.g. Gaedike 1980; Leraut 2012; Slamka 2013) and is therefore not redescribed here.

Udea delineatalis (Walker in Melliss 1875)

Figs 1, 11, 21, 28

Scopula delineatalis Walker in Melliss 1875: 189. Type locality. St. Helena.

Material examined. ***Cotype*:** Saint Helena • ♀; "St Helena. Wollaston Coll. 79–68.", [round label with green border] "Type"; unique specimen identifier NHMUK010209954; NHMUK. **Additional material:** Saint Helena • 1 ♂ 5 ♀♀; Napoleon's Tomb; 15°57.4733'S, 5°41.91'W; 540 m a. s. l.; 11 Apr. 2018; T. Karisch & A.-J. Dutton leg.; mixed non-native forest, light catch with 250 W HQL • 1 ♂; same collection data as for preceding; genitalia dissection no. 3945, Karisch 2022; SDEI, MNVD • 3 ♀; Bevins Gut bei [near] Crack Plain, 3.6 km SSW Jamestown; 15°57.0667'S, 5°44.2323'W; 460 m a. s. l.; 28 Dec. 1995; T. Karisch leg.; felsiges, gebüschreiches Tal, kl. Weideflächen [rocky, shrub-rich valley, small grazing areas], light catch with 125 W HQL; DNA voucher MTD Lep356; MNVD, SDEI • 1 ♀; same collection data as for preceding; DNA voucher MTD Lep248; SMTD • 1 ♀; SW Steilhang [steep slope] Cuckhold's Point, 5.25 km SSO Jamestown; 15°58.0167'S, 5°42.4167'W; 780 m a. s. l.; 24 Dec. 1995; T. Karisch leg.; *Dicksonia arborescens-Melanodendron integrifolium*-Sisalflur [sisal meadow], light catch with 125 W HQL; SDEI • 3 ♀♀; SO-Hang [SE slope] Rose Hill, 5.6 km SSO [SSE] Jamestown; 15°48.0667'S, 5°42.0167'W; 640 m a. s. l.; 27 Dec. 1995; T. Karisch leg.; Sisalflur [sisal meadow], *Acacia longifolia*-reiche Gehölze [*Acacia longifolia*-rich groves], light catch with 125 W HQL; SDEI • 1 ♀; Fisher's Valley nordöstlich [northeast of]

Tobacco Plain, 5.4 km SO [SE] Jamestown; 15°57.1'S, 5°46.8333'W; 380 m a. s. l.; 23 Dec. 1995; T. Karisch leg.; lückige Trockengebüsche, grasreiche Bachaue [gappy dry scrubs, grass-rich stream meadow], light catch with 125 W HQL; SDEI • 1 ♀; Hooper's Rock; 15°59.4933'S, 5°44.515'W; 690 m a. s. l.; 26 Mar. 2018; T. Karisch leg.; *Ulex*-rich shrubland on rocks, light catch with 250 W HQL; SDEI • 1 ♀; Black Gate Nursery, 0.1 km WSW; 15°58.3917'S, 5°41.94'W; 755 m a. s. l.; 16 Apr. 2018; T. Karisch leg.; *Dicksonia-Melanodendron* thicket, light catch with 250 W HQL; SDEI.

Diagnosis. Similar to *U. ferrugalis* (Fig. 2), but forewings more triangular, apex not as acute, postmedian field more grey, antemedian line not as sharply angulated in the middle; hindwing with distinctive broad greyish brown marginal field, postmedian line also visible in anal area. In male genitalia, the apical margins of the juxta of *U. delineatalis* (Fig. 21) do not have projections as in *U. ferrugalis* (Fig. 22), and the cornutus of the phallus has a blunt and not rounded tip. In the female genitalia of *U. delineatalis* (Fig. 28), the distal, cup-shaped part of the antrum is wider at the transition to the short stalk-like section than in *U. ferrugalis* (Fig. 29).

Description of adults. ***Head*:** Orange; labial palps about three times as long as eyes, covered with long scales, orange, ventrally whitish, third segment short, greyish-brown; maxillary palps ochre, speckled with grey, long enough to touch each other at apex; haustellum about 5 mm long, basally covered with whitish scales. Antenna filiform, ciliate in male and female, flagellum orange, intermixed with brown scales. ***Thorax*:** Greyish orange. Tibia of fore- and midlegs slightly ochre brown, of hindlegs whitish, outer tibial spur pair of midlegs and proximal spur pair of hindlegs with outer spur about half as long as inner spur, distal spur pair of hindlegs with outer spur about 4/5 length of inner spur. ***Wings*:** (Fig. 1) Forewing length of male 9.5 mm, of females 8–9 mm. Forewings of orange brown ground colour, suffused with grey. Antemedian line grey, obtuse angled in middle, outward angled just before dorsum. Proximal discoidal stigmata oval or ellipsoid, distal discoidal stigmata narrow, often divided by a grey line in the middle; space between proximal and distal stigmata often less grey tinged. Postmedian line fine, grey, dentate, convex curved from costa to CuA1, with abrupt dent inward at CuA2, then continuing slightly dentate towards dorsum by reaching it at right angle. Distal area along postmedian line and along margin less greyish. Marginal line black, disrupted at veins. Fringes orange-brown, with a broader grey transversal line. Underside pale yellowish, discoidal stigmata, veins, and marginal area grey; postmedian line dark grey, visible from costa to CuA1. Hindwing pale yellowish, anal area slightly greyish dusted. Discoidal spot conspicuous, dark grey. Postmedian line greyish brown, very fine and dentate between M2 and CuA2. Marginal band greyish brown, broad, paler towards anal angle. Fringes whitish, with a grey postbasal fascia and grey tips. Underside whitish, marginal area slightly dusted with grey, darker grey strigulae between veins; postmedian line broken into patches. Outer discoidal spot large, blackish, round; upper discoidal spot comma-shaped, grey. ***Abdomen*:** Greyish ochreous, distal margins of tergites whitish; tip pale orange; ventral side of abdomen pale yellowish. Tympanal organs (Fig. 11) with lobulus well developed, broad. ***Male genitalia*:** (Fig. 21) Uncus tip rounded, covered with stronger bristles, bulbous thickening at basis; tegumen roughly rectangular; transtilla arms broad triangular; vinculum U-shaped, saccus quite broad; juxta large, plate-like, basal somewhat rounded, narrowed apical, with a straight but irregular margin. Valvae long, slender in distal part, narrowest at half of costa; costa curved; cucullus rounded; fibula present, strong and long with a broader basis. Phallus slender, with a broad, sclerotized cornutus with a blunt tip; at tip of the uneverted vesica a dense group of small, less sclerotised spines. ***Female genitalia*:** (Fig. 28) Papillae anales simple, with long chaetae. Apophyses posteriores slender, more or less straight; apophyses anteriores about 1.5-times as long as apophyses posteriores, thicker, wid-

Figures 1–5. Adults of Afrotropical *Udea* species. **1.** *U. delineatalis* (Walker in Melliss 1875); **a.** ♂ (SDEI); **b.** cotype ♀ (NHMUK); **2.** *Phlyctaenia epicoena* Meyrick, 1937 syn. nov. of *U. ferrugalis* (Hübner, 1796), paralectotype ♀ (NHMUK); **3.** *U. hageni* Viette, 1952, ♂ (NHMO); **4.** *U. kirinyaga* Mally, sp. nov., holotype ♂ (NHMO); **5.** *U. momella* Mally, sp. nov., holotype ♂, abdomen removed (ZSM). Scale bar represents 5 mm, all specimens to scale.

est at a triangular bulge at 1/3 length from base, distal half slightly curved dorsad. Antrum simple, sclerotised, broadly funnel-shaped with posterior 2/3 with slightly tapering sides towards anterior, then sharply constricting into the narrower funnel-shaped anterior third that is about as long as broad. A very short membranous section leads to colliculum; colliculum tubular, slightly tapering towards anterior, twice as long as broad, sclerotised except for a broad longitudinal membranous dorsal strip. Ductus bursae membranous, somewhat longer than, and about as wide as colliculum, posterior half leading laterally into a small bulge, then running anteriad, producing an angle in the course of ductus. Ductus ejaculatorius attached at posterior end of ductus bursae, near colliculum. Corpus bursae large, ovate, membranous apart from signum. Signum large, dentate, longitudinally oriented, broadest at half its length, posterior signum arm with concave sides drawn out long into an acute tip, anterior arm broad, concave near to signum centre, convex along distal 2/3, ending in a broad-angled tip.

Distribution. Only known from the mid-Atlantic island of Saint Helena.

Biology. The larval hostplant remains to be determined. The species can be attracted by night with 125 W and 250 W mercury vapour (HQL) lamps. The investigated material consists almost exclusively of females, with only one male present among the 17 specimens, suggesting that males could be less attracted by light. The material was collected at elevations ranging from 380 to 780 m above sea level in various habitats, such as mixed non-native forest, rocky, shrub-rich valleys with small pastures, *Ulex*-rich shrubland on rocks, vegetation mosaics formed by *Phormium tenax* and *Acacia longifolia*, and *Dicksonia-Melanodendron* thicket of the cloud forest zone.

Genetic data. A single DNA Barcode (COI-5P) sequence is available of *U. delineatalis*, published in Mally and Nuss (2011) as part of the 1,434 basepair sequence of the mitochondrial *COI* gene GenBank accession number JF497043). The DNA Barcode is placed in the BOLD BIN (Barcode Index Number) BOLD:AAC3729 – the same BIN as *U. ferrugalis* and the Asian *U. testacea* (Butler, 1879), although all three species are clearly distinguishable morphologically.

Remarks. Unlike *U. hageni*, which is endemic to the mid-Atlantic Tristan da Cunha Island, *U. delineatalis* shows no wing reduction. Apart from *U. delineatalis*, *U. ferrugalis* was also recorded from St. Helena (Walker in Melliss 1875), although it has not been found there in the past decades (pers. obs. T. Karisch).

Udea ferrugalis (Hübner, 1796)

Figs 2, 12, 22, 29

Pyralis ferrugalis Hübner, 1796: 27–28, pl. 9 fig. 54. Type locality: Hungary.
= *ferruginalis* (Rossi, 1794) (misspell.).
= *feruginalis* Taylor, 1951 (misspell.).
= *Phlyctaenia epicoena* Meyrick, 1937 syn. nov. Type locality: DR of the Congo [Belgian Congo], Lubumbashi [Elisabethville].
= *Pionea granjalis* Chrétien, 1925. Type locality: Spain.
= *Pionea maculata* Costantini, 1923 (infrasubsp.). Type locality: Italy.
= *Pionea obsoleta* Costantini, 1923. Type locality: Italy.
= *Scopula hypatialis* Walker, 1859. Type locality: Sri Lanka [Ceylon].
= *Scopula martialis* Guenée, 1854. Type locality: Ethiopia [Abyssinie].
= *Udea martialis* f. *fusca* Dufrane, 1960. Type locality: France, Pyrénées, Lannemezan.
= *Udea martialis* f. *pallida* Dufrane, 1960. Type locality: Morocco, Rabat.

Material examined. Paralectotypes of *Phlyctaenia epicoena*, Meyrick, 1937: Democratic Republic Of The Congo • ♀; "Belgian Congo" [DR Congo], "Elisabethville" [Lubumbashi]; 18 Feb. 1835; "Meyrick Coll. B.M. 1838-290."; "*Phlyctaenia epicoena* $^{2}/_{2}$ Meyrick E. Meyrick det. in Meyrick Coll.", "Paralectotype *Phlyctaenia epicoena* Meyr Det. K.Maes 1995"; NHMUK014047387; NHMUK • ♀; "Belgian Congo" [DR Congo], "Elisabethville" [Lubumbashi]; 5 Jan. 1835; "Meyrick Coll. B.M. 1938–290", "*Phlyctaenia epicoena* $^{1}/_{2}$ Meyrick E. Meyrick det. in Meyrick Coll.", "Paralectotype *Phlyctaenia epicoena* Meyr. Det. K.Maes 1995."; "epicoena Meyr." [in Meyrick's handwriting]; NHMUK010921399, genitalia dissection number NHMUK010316679; NHMUK. **Additional material:** Kenya • 1♂; Kenia [Kenya], Kabete; 1–20 Sep. 1972; H. Politzar leg.; Mally genitalia dissection no. 1179; ZSM • 1♂; same data as for preceding; Mally genitalia dissection no. 1183; ZSM • 1♀; same data as for preceding; Mally genitalia dissection no. 1180; ZSM • 1♀; same data as for preceding; Mally genitalia dissection no. 1186; ZSM • 1 ♂; Kenia [Kenya], Nairobi, Karura Forest; 24–27 Apr. 1973; H. Politzar leg.; Mally genitalia dissection no. 1184; ZSM • 1 ♀; same data as for preceding; Mally genitalia dissection no. 1185; ZSM. – SOUTH AFRICA • 1 ♀; Transvaal, Mooisplaats, Bronkhorstspruitlist; Sep. 1949; Koch leg.; Mally genitalia dissection no. 1176; ZSM • 1 ♀; same data as for preceding; Mally genitalia dissection no. 1177; ZSM.

Distribution. Afrotropical realm: Ascension Island, Botswana, Burundi, Cape Verde, Comoros, Democratic Republic of the Congo, Eritrea, Eswatini, Ethiopia, Kenya, Lesotho, Madagascar, Mauritius, Mozambique, Namibia, Oman, Réunion, Seychelles, South Africa, Sudan, Yemen, Zambia, Zimbabwe (Butler 1894; Hampson 1898; Joannis 1927; Rebel 1930; Ghesquière 1942; Viette 1954, 1957, 1958; Martin 1956; Amsel 1963; Legrand 1966; Kopij 2006; Martiré and Rochat 2008; GBIF 2022; iNaturalist 2022; SDEI; summarised in De Prins and De Prins 2011–2022); the record from Saint Helena is doubtful (Wollaston 1879). **Palaearctic realm:** Algeria, Israel, Morocco, Saudi Arabia, Tunisia, all Europe, incl. Azores, Canary Islands, China, Iran, Japan, Korea, Pakistan, Russia (Amsel 1965, 1966; Speidel and Hassler 1989; Báez and Martín 2004; Borges et al. 2005; GBIF; iNaturalist). **Oriental realm:** China, India, Taiwan, Vietnam (Toll 1948; Zhang and Li 2016; iNaturalist).

Biology. The species is polyphagous, i.e., feeding on plants of various plant families. Robinson et al. (2010) list host genera from nine families, although records from the Oriental region might be misidentifications of *U. testacea* (see "Genetic data" below and Discussion). Palaearctic records comprise *Beta vulgaris* (Amaranthaceae), *Cichorium intybus* (Asteraceae), *Capsicum*, *Solanum lycopersicum* and *S. melongena* (Solanaceae) as well as *Cucurbita* (Cucurbitaceae). In South Africa, the caterpillars feed on *Lepidium capense* Thunb. (Brassicaceae) according to Taylor (1951) and on *Erigeron* (Asteraceae) according to Robinson et al. (2010). More information about the biology of *U. ferrugalis* can be found in Gaedike (1980) for Central Europe, and in Lee et al. (1999, 2002) for East Asia. The species is known to be an occasional migrant (Lempke 1967).

Genetic data. Numerous DNA Barcode (COI-5P) sequences (n=41 with DNA Barcodes) are publicly available for *U. ferrugalis* on BOLD Systems. A genetic distance analysis of the data with Kimura 2-paramater model results in an intraspecific variation ranging from 0% to 2.42%. The relatively large maximum distance is most likely due to several species that appear to be misidentified as *U. ferrugalis*:

Two specimens with specimen IDs BC MTD 01830 (collected in Nankai, China) and NIBGE MOT-03061 (collected in Khyber Pakhtunkhwa, Pakistan) appear to be misidentifications of *U. testacea*, as both DNA Barcode sequences are a 99.69–100% match with the *COI* sequence of *U. testacea* published by Matsui and Naka (2021).

Another specimen with the specimen ID BIOUG25981-C06, collected in Laikipia, Kenya (see "?" in Fig. 35), has a maximum of 98.27% sequence similarity with other barcoded *Udea* specimens. It can currently not be associated with any known *Udea* species and may represent an undescribed species that should be further investigated. Unfortunately, the (female) specimen was caught in a Malaise trap, resulting in the complete loss of its wing maculation. Additional material, ideally including males, will be necessary to determine its identity.

Udea ferrugalis shares its BOLD BIN (BOLD:AAC3729) with *U. delineatalis* and the Asian *U. testacea*. Mutuura (1954) considered *U. testacea* a bona species based on genitalia morphology and removed it from synonymy (Shibuya 1928) with *U. ferrugalis*. Only one DNA Barcode is available for *U. testacea* (published by Matsui and Naka 2021), and one for *U. delineatalis* (published by Mally and Nuss 2011). More data is needed to make a more conclusive statement on the species boundaries based on DNA Barcode data (Meier et al. 2021).

Remarks. Externally, the paralectotype of *Phlyctaenia epicoena* is indistinguishable from *U. ferrugalis*. Investigation of the female genitalia (prep. no. NHMUK010316679) indicates that the specimen furthermore agrees with *U. ferrugalis* in the typical calyx-shaped antrum, with the

anterior fourth marked-off as a short, thinner stalk, in the sclerotised tubular colliculum, twice as long as broad and with the sclerotisation leaving out a longitudinal band of membranous wall, in the short, thin ductus bursae with a small round projection near its posterior end (one of the two synapomorphies for the *U. ferrugalis* genus group sensu Mally and Nuss 2011), and in the shape, size and position of the ediacaroid signum (sensu Mally et al. 2019). We thus consider *Udea epicoena* (Meyrick, 1937) conspecific with *U. ferrugalis* and synonymise it: *Phlyctaenia epicoena* Meyrick, 1937 syn. nov. of *Udea ferrugalis* (Hübner, 1796). Consequently, we did not include *Ph. epicoena* in the phylogenetic analyses, as *U. ferrugalis* is already present among the data.

Udea hageni Viette, 1952

Figs 3, 13, 23

Udea hageni Viette, 1952: 3–5, figs 1, 2. Type locality: Tristan da Cunha.

Material examined. Tristan Da Cunha • 1 ♂; "St.75", "Gm 1075 ZM.Oslo", "*Udea hageni* VH."; DNA voucher ZMBN Lep520; Mally genitalia dissection no. 1161; NHMO.

Diagnosis. The species is readily distinguished from other *Udea* species by the narrow, apically pointed fore- and hindwings, more reminiscent of some Tortricidae than of Spilomelinae.

Description of adults. ***Head*:** Dorsally greyish-white with interspersed brownish scales, ventral side beige; labial palps porrect, elongate triangular, about twice as long as eye diameter, dorsal and outer sides brown, ventral and inner sides as well as outer side's base of first meron and a narrow ventral area on second meron beige; maxillary palps brown, well developed, long enough to touch each other at apex, terminal meron with spatulate brush of long scales; haustellum fully developed, basally with cream-coloured scales; frons greyish-brown, slightly rounded; compound eyes large, hemispherical; antennae ochre-brown, scapus short, hidden in scales of vertex, pedicellus large, somewhat swollen, flagellum in male anteroventrally with dense ciliation almost half as long as flagellum width; vertex in centre and behind ocelli with tuft of long cream-coloured scales. ***Thorax*:** Prothorax, tegulae, forelegs and anterior mesothorax brown, posterior mesothorax, metathorax and mid- and hindlegs light grey. Outer tibial spur 2/3 length of inner spur in midleg, half as long as hindlegs' proximal spur pair, and almost as long as inner spur in distal spur pair. ***Wings*:** (Fig. 3) Forewing length of male 8 mm. Wings with reduced area compared to other *Udea* species. Male with single frenulum bristle, condition unknown for female. Forewing slender, with long convex costal margin, acute apex of about 60°, relatively short, straight termen, and short, convex anal margin. Ground colour cream-beige, with broad straight streak of brown colour from forewing base to 2/3 length of forewing in direction of termen-anal angle, second streak from basal of proximal discal stigma over distal stigma, broadening to area between forewing's apex and mid-termen; discoidal stigmata dark brown, proximal discoidal stigma oval, distal stigma a less clearly defined larger spot on anal side of second brown straight forewing streak; no antemedial line present, postmedial line very vague, as an outward-arching line from beyond distal discoidal stigma to distal end of broad straight streak from wing base; distal costa and termen at ends of wing veins with streak-like dark brown dots; fringe cream-coloured. Hindwing ground colour cream-beige, distal area suffused with grey-brown, veins brownish; faint brownish discoidal stigmata, connected by a

thin brownish line; termen and anal margin with interrupted brown line; fringe cream-coloured. Underside of forewing more or less uniformly beige-grey, with upper side's broad streak from wing base as well as distal discoidal stigma as somewhat darker areas; ends of wing veins with streak-like dark brown dots; fringe pale beige; underside of hindwing uniformly pale beige, with small central brown discal spot; vein ends and fringe as in forewing underside. ***Abdomen*:** Dark to light grey. Tympanal organs (Fig. 13) with lobulus absent. ***Male genitalia*:** (Fig. 23) Circular uncus head with stiff bifid, anteriad directed chaetae on dorsal surface, neck slender, elongate, base of uncus broadly attached to tegumen and each side with a small laterad protrusion and notch at attachment to tegumen; tegumen rectangular; transtilla arms short, rounded, far apart from each other; vinculum large, together with saccus forming an oval; saccus broad U-shaped; juxta small, broadly drop-shaped, dorsally with V-shaped longitudinal membranous "notch" reaching mid-length; valvae elongate, slender, tapering towards apex; costa concave, base broad, slightly inflated, valva apex evenly rounded, ventral valva margin concave in apical half, at sacculus convex; sacculus elongate, ventrodistal tip in close association to central fibula, distal edge straight; fibula emerging near costa base from an elongate base, forming slender posteriad claw-like structure reaching towards distal edge of sacculus, not reaching ventral margin of valva. Phallus slender, thinnest at posterior end, anterior end stout, without coecum; central section with somewhat stronger sclerotisation; posterior tip of phallus apodeme ventrally with short triangular tooth; vesica with short, slender, spine-shaped cornutus. ***Female genitalia*:** Unknown.

Distribution. Only known from the mid-Atlantic island of Tristan da Cunha.

Genetic data. Not available.

Remarks. Based on the male genitalia illustrated in Viette (1952), Mally and Nuss (2011) placed *Udea hageni* in the *U. ferrugalis* species group. However, examination of a specimen and the results of our phylogenetic analysis suggest that the species is a lineage of the *U. numeralis* species group. So far, *U. hageni* is the only island-endemic *Udea* species with marked wing reduction. To our knowledge, the female sex of this species is still unknown.

Udea kirinyaga Mally, sp. nov.

https://zoobank.org/D6C1D697-8266-48A6-8B1E-FA62B7C13E7A

Figs 4, 14, 24

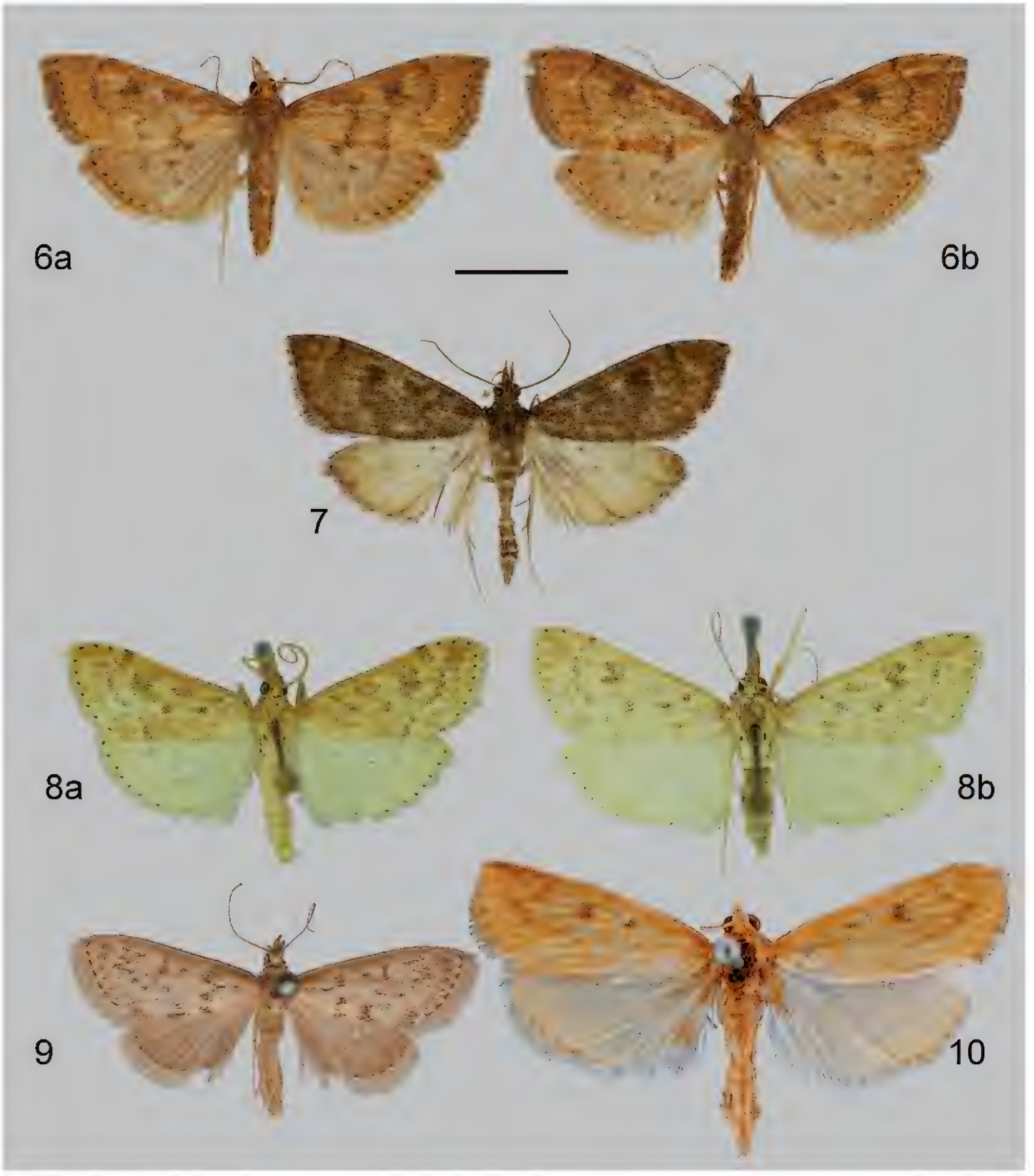
Type locality. Kenya, Central Province, Mt. Kenya southern slope, Castle Forest Lodge, 0°22'51"S, 37°18'34"E, 2070 m.

Material examined. ***Holotype*:** Kenya • 1 ♂; Central Province, Mt. Kenya southern slope, Castle Forest Lodge; 2070 m a. s. l.; 0°22.85'S, 37°18.5667'E; 5–7 Dec. 2010; L. Aarvik & D. Agassiz leg.; DNA voucher ZMBN Lep135; Mally genitalia dissection no. 950; unique specimen identifier NHMO 612835; NHMO.

Diagnosis. *Udea kirinyaga* is clearly distinct in maculation from *U. ferrugalis* (Fig. 2), *U. delineatalis* (Fig. 1) and *U. meruensis* (Fig. 7), most prominently so in the postmedial line, which runs from the costa inwards towards the distal discoidal stigma, whereas in the other species this part of the postmedial line softly bends towards the termen. *Udea kirinyaga* has a superficial

resemblance to *Achyra melanostictalis* (Fig. 9), but the forewing ground colour is more yellowish, with a weak ante- and postmedial lines, and a broad diffuse subterminal band; the hindwings are pale cream-white apart from the outer margin and have a diffuse discal spot. In the male genitalia, *U. kirinyaga* (Fig. 24) is distinguished from *U. meruensis* (Fig. 26) in the rounder, U-shaped saccus, the more elongate juxta with straight sides, and the claw-shaped, pointed main cornutus in the phallus. It is distinguished from *U. ferrugalis* (Fig. 22) by the shape of the main cornutus, which is blunt and thumb-shaped in *U. ferrugalis*; furthermore, *U. ferrugalis* exhibits strongly sclerotised "horns" on each side of the juxta apically. The species is distinguished from the Eurasian *U. accolalis* by the fibulae, which are shorter and straighter in *U. accolalis* (see e.g., Slamka 2013, pl. 21).

Description of adults. ***Head*:** Brownish-beige; labial palps porrect, triangular, extending forward somewhat longer than eye diameter, dorsal and outer sides brown, darker at eye, ventral and inner sides as well as outer side's base of first meron and a narrow ventral area on second meron beige; maxillary palps well developed but short, barely long enough to touch each other at apex, base dark brown, terminal meron with spatulate brush of beige scales; haustellum fully developed, basally with cream-coloured scales; frons beige, flatly rounded; compound eyes large, hemispherical; antennae ochre-brown, scapus short, pedicellus large, somewhat swollen, flagellum in male anteroventrally with dense ciliation about one third the flagellum width; vertex in centre and behind ocelli with tuft of long cream-coloured scales. ***Thorax*:** Prothorax and tegulae ochre-brown, meso- and metathorax as well as legs beige, fore- and midlegs with front of femur and tibia brownish. Midleg with outer tibial spur half as long as inner, hindlegs' proximal spur pair with inner spur very long, outer spur minute, distal spur pair with outer spur 2/3 length of inner one. ***Wings*:** (Fig. 4) Forewing length of male 11 mm. Single frenulum bristle in male, condition unknown in female. Forewings with ochre to cream-brown ground colour. Faint brownish antemedian line leaving costa at 1/5 obliquely outward, after 1/3 abruptly directed straight towards anal margin. Discoidal stigmata dark brown, proximal one small, circular, distal one larger, roughly circular to short comma-shaped. Anal centre of wing with a slightly darker half-circle, slightly skewed towards – and almost reaching – proximal discoidal stigma. Postmedian line brown, only costal part clearly formed, where it leaves the costa at 2/3 straight inward towards distal end of distal discoidal stigma, then too faded to trace. Subterminal line a broad diffuse brown band slightly arching inwards from subapex to subtornus, on terminal side fading into subterminal area; subterminal area a lighter ochre than in proximal wing, suffused with brown scales; apical costa with two brown markings, one in apex and one slightly more proximal on costa. Veins on outer margin marked with brown dots. Brownish fringe. Hindwing ground colour cream; diffuse brown proximal discoidal stigma, indistinct distal discoidal stigma with a very faint postmedian line connecting it to the costa. Outer margin blurred light brown, broad at apex, narrowing towards tornus; veins on outer margin with dark markings; fringe a lighter brown than in forewing. Ventral wing sides like dorsal sides, but somewhat darker and maculation more contrasted, with area proximal of postmedian line dark brown versus lighter brown area distal of it, and subtornal area cream; postmedian line in hindwing continued below distal discoidal stigma as line of dark brown dots trailing off towards anal area. ***Abdomen*:** Ochre to cream-brown like forewing ground colour, first segment and posterior end of mid-segments cream-coloured like hindwings. Tympanal organs (Fig. 14) with lobulus well developed, almost as long as broad. ***Male genitalia*:** (Fig. 24) Ovate uncus head with stiff bifid, anteriad directed chaetae on dorsal surface, neck slender, elongate, base of uncus broadly attached to tegumen and each side with a small dorsolaterad protrusion, connection to tegumen laterally notched; tegumen roughly rectangular, ventrally somewhat widening; transtilla with wide round-



Figures 6–10. Adults of Afrotropical *Udea* species and species removed from *Udea*. **6.** *U. nicholsae* Mally, sp. nov., **a.** holotype ♀ (ZSM); **b.** paratype ♀ (ZSM); **7.** *U. meruensis* Mally, sp. nov., holotype ♂ (NHMO); **8.** *U. namaquana* Karisch & Mally, sp. nov., a) holotype ♂ (SDEI), b) paratype ♀ (SDEI); **9.** *Achyra melanostictalis* (Hampson in Poulton 1916), lectotype ♀ (OUMNH); **10.** *Lirabotys infuscalis* (Zeller, 1852), holotype ♂ (NHRS). Scale bar represents 5 mm, all specimens to scale.

ed base and elongate triangular arms, dorsal margin folded over; vinculum large, together with saccus forming an oval; saccus broad U-shaped, with a sharp short ventrad keel and a transverse arch dorsal of keel; juxta large, plate-like, roughly hexagonal, with narrow longitudinal membranous "notch" in

ventral half medially; valvae long, elongate, slender, narrowest at ca. 2/3 of costa from costa base; costa straight, apex obtusely rounded, ventral valva margin concave in apical half, at sacculus convex; sacculus broad elongate, with a broad triangular protuberance reaching base of costa and close to base of fibula; fibula emerging near costa base from a triangular base, forming a slender ventrad fang-like structure bending away from sacculus base, not reaching ventral valva margin. Phallus slender, thinnest in mid-section, anteriorly with very short coecum; vesica with short, claw-shaped cornutus emerging from a drop-shaped base, and with a broad field of numerous tiny cornuti posteriad of large cornutus (in uneverted vesica). ***Female genitalia*:** Unknown.

Distribution. So far only known from the type locality, Mount Kenya in Kenya.

Etymology. The species is named after Kirinyaga, the Kikuyu name for Mount Kenya.

Genetic data. The DNA of the holotype was extracted and is stored as Lepidoptera DNA sample no. 135 in the DNA collection of the ZMBN. 1,459 base pairs of the mitochondrial *COI* gene (GenBank accession number ON206730) and 363 base pairs of the nuclear *wingless* gene (GenBank accession number ON206634) have been sequenced from that DNA sample to be included in the phylogenetic analysis. A search against the *COI* full database on BOLD resulted in two closest matches of 97.22% similarity of two unidentified *Udea* specimens, one from Gauteng, South Africa (Sample ID BIOUG08930-B05) and the other from W-Bulgaria (Sample ID BIOUG15079-B07). The next-closest matches are of *U. ferrugalis* at 96.19–96.3%, of *U. delineatalis* at 96.25% and of *U. stellata* (Butler, 1883) at 96.19%.

Remarks. The species is placed in the *U. ferrugalis* species group (sensu Mally and Nuss 2011) based on the males exhibiting one of the two apomorphies for the group: the presence of a cluster of small cornuti on the vesica. The second apomorphy concerns female genitalia, which are not available for study at this time.

Udea momella Mally, sp. nov.

https://zoobank.org/A882D330-9C3A-4885-821B-36FD40C03BDB

Figs 5, 15, 25

Type locality. Tanzania, Arusha Region, Mount Meru, Arusha National Park, Momella, 1600–1800 m.

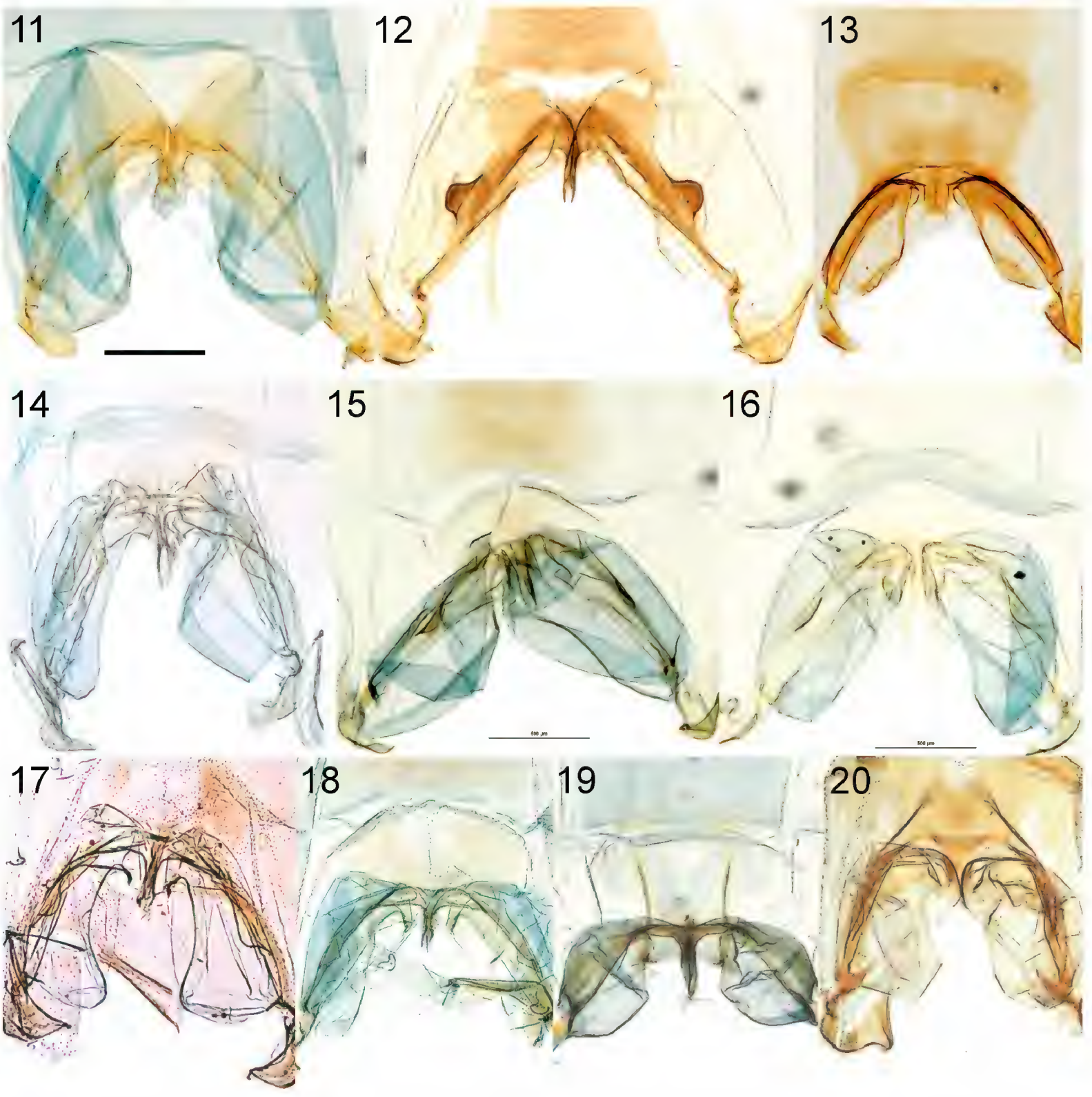
Material examined. ***Holotype*:** Tanzania • 1 ♂; Tanganyika sept. [N Tanzania], Mount Meru, Momella; 1600–1800 m a. s. l.; 10–19 Feb. 1964; W. Forster leg.; Mally genitalia dissection no. 1187; ZSM.

Diagnosis. Externally, the single known specimen resembles most closely *U. ferrugalis* (Fig. 2). Forewing colouration is not a reliable character distinguishing the two species, as *U. ferrugalis* can be similarly coloured. *Udea momella* is best distinguished by the forewing postmedian line, which is a long wide arch spanning from 3/4 length of the costa to about 2/3 length of anal margin, more resembling the forewing pattern of certain Pyraustinae such as *Achyra nudalis* (Hübner, 1876) than that of *Udea*; in *U. ferrugalis*, the forewing postmedian line usually forms a wide half-circle around the distal discoidal stigma that leads into an oval loop on the anal side of that stigma before running towards the anal margin. Furthermore, the forewing costa is mostly straight and slightly curved in the distal 1/4, giving the wing apex and the entire forewing a more triangular shape, whereas in *U. ferrugalis* the distal 1/3 of the forewing costa forms a long curve, resulting in an

overall slenderer forewing shape. In *U. momella*, the hindlegs' proximal spur pair has a minute outer spur, whereas in *U. ferrugalis* this spur is well developed and about half as long as the inner spur.

It is also very close to *U. ferrugalis* in the male genitalia, especially in the shape of uncus, juxta, phallus and cornutus. The clearest differences between the two species are in the orientation of the fibula – ventrad in *U. ferrugalis* (Fig. 22) –, and in the shape of the fibula base, which is as long as the fibula that is protruding from it in *U. momella* (Fig. 25), while the base is only half as long as the fibula in *U. ferrugalis*.

Description of adults. ***Head*:** Dorsal side ochre-brown, ventral side beige; labial palps porrect, stretched triangular, about twice as long as eye diameter, dorsal side ochre-brown, ventral side beige, laterally with first meron and a narrow ventral area on second meron beige; maxillary palps well developed, long enough to touch each other at apex, terminal meron with spatulate brush of long scales; haustellum fully developed, basally with cream-coloured scales; frons ochre-brown, margins beige, flatly rounded; compound eyes large, hemispherical; antennae ochre-brown, scapus short, hidden in scales of vertex, pedicellus large, somewhat swollen, flagellum about 2/3 length of forewing, anteroventrally with short dense ciliation; vertex in centre and behind ocelli with tuft of long beige and cream-coloured scales, neck dorsally with a crest of a few broadly spatulate scales. ***Thorax*:** Ochre-brown dorsally, beige-cream ventrally. Tegulae large, ochre-brown, with lighter brown tip. Legs beige-cream, foreleg with tibia and proximal tarsus with brownish scales. Outer tibial spur half as long as inner spur in midleg, in hindleg distal spur pair with outer spur 2/3 length of inner spur, proximal pair with long inner spur, spanning most of its tarsus segment's length, and minute, barely visible outer spur, mostly hidden by leg scales around spur (only one hindleg preserved on holotype). ***Wings*:** (Fig. 5) Forewing length of male 8 mm. Frenulum bristle in male appears to consist of two fused bristles. Forewings with light brownish-orange ground colour, interspersed with brownish scales; costa somewhat darker. Very faint diffuse brownish antemedian line in first quarter of forewing. Proximal discoidal stigma not evident, distal one a diffuse, roughly circular brownish spot. Postmedian line brownish, leaves costa at about 3/4 in an arc around distal discoidal stigma before continuing straight towards 2/3 of anal wing margin. Subterminal area a narrow light orange band devoid of interspersed brownish scales. slightly arching inwards from subapex to subtornus, on terminal side fading into subterminal area. Veins on costa apex and outer margin marked with dark brown dots. Outer fringe basally light orange, followed by a brown line at about 1/3 fringe width, outer 2/3 light brown. Hindwing dorsally with cream ground colour, with veins light orange; proximal discoidal stigma absent, distal discoidal stigma a small brown dot. Postmedial line a diffuse brownish line leaving costa at about 2/3, circling distal discoidal stigma, fading out towards anal margin. Outer margin light brown, broad at apex, narrowing towards tornus; veins on outer margin with dark markings; fringe light orange, much like in forewing's subterminal area. Ventral wing sides: forewing ochre with brownish subcostal streak, diffuse but clear brown distal discoidal spot, brownish postmedial line in costal half of wing, and clear dark brown dots on vein ends of apical costa and termen; fringe as on dorsal side. Hindwing whitish, semi-transparent, ochre costal band, apex and veins, small brownish discoidal spots, brown postmedial line in costal half of hindwing, vein ends and fringe as on dorsal side. ***Abdomen*:** Colour of abdomen not investigated prior to genitalia dissection. Tympanal organs (Fig. 15) with lobulus well developed, almost as long as broad. ***Male genitalia*:** (Fig. 25) Ovate uncus head with stiff bifid, anteriad directed chaetae on dorsal surface, neck slender, elongate, lateral sides sparsely set with stiff chaetae, base of uncus broadly attached to tegumen and each side with a small dorsolaterad



Figures 11–20. Tympanal organs of Afrotropical *Udea* species and species removed from *Udea*. **11.** *U. delineatalis* (Walker in Melliss 1875), ♂; **12.** *U. ferrugalis* (Hübner, 1796), ♂; **13.** *U. hageni* Viette, 1952, ♂; **14.** *U. kirinyaga* Mally, sp. nov., ♂; **15.** *U. momella* Mally, sp. nov., ♂; **16.** *U. nicholsae* Mally, sp. nov., ♀; **17.** *U. meruensis* Mally, sp. nov., ♂; **18.** *U. namaquana* Karisch & Mally, sp. nov., ♂; **19.** *Achyra melanostictalis* (Hampson in Poulton 1916), ♀; **20.** *Lirabotys infuscalis* (Zeller, 1852), ♂. Scale bar represents 500 µm, all figures to scale.

protrusion, connection to tegumen laterally notched; tegumen broad, approximately rectangular; vinculum large, together with saccus forming a broad U; saccus broad, U-shaped; juxta large, sclerotised, basal part roughly circular to hexagonal, distal part with parallel sides that taper into a pair of slender ventrad processes, forming a broad U-shaped central recess; valvae long, elongate, slender, narrowest around half costa length; costa slightly concave, apex obtusely rounded, ventral valva margin concave in apical half, at sacculus convex; sacculus large, roughly triangular, dor-

sal corner closely approaching base of fibula and costa; fibula emerging alongside basal from an elongate base, forming slender fang-like structure bending towards centre of genitalia in situ (but pointing dorsad in the embedded genitalia preparation). Phallus evenly sclerotised, slender, thinnest in mid-section, anteriorly with short coecum; vesica with short, blunt cornutus emerging from an elongate base, further posterior with a sclerotised dentate area. ***Female genitalia*:** Unknown.

Distribution. So far only known from the type locality on the eastern side of Mount Meru in Tanzania.

Etymology. The species is named after Momella, the type locality located on the eastern flank of Mount Meru.

Genetic data. Not available.

Remarks. The species is placed in the *U. ferrugalis* species group (sensu Mally and Nuss 2011) based on the male exhibiting one of the two apomorphies for the group: the presence of a cluster of small cornuti on the vesica. The second apomorphy concerns female genitalia, which are not available for study at this time.

Udea nicholsae Mally, sp. nov.

https://zoobank.org/5A9A9ADD-6405-4767-9D24-D4ABF7163A08

Figs 6, 16, 30

Type locality. Tanzania, Arusha Region, Mount Meru, Arusha National Park, Momella, 1600–1800 m.

Material examined. ***Holotype*:** Tanzania • 1 ♀; Tanganyika sept. [N Tanzania], Mount Meru, Momella; 1600–1800 m a. s. l.; 10–19 Feb. 1964; W. Forster leg.; Mally genitalia dissection no. 1171; ZSM • ***Paratype*:** 1 ♀; same data as for holotype; 11–20 Jan. 1964; Mally genitalia dissection no. 1172; ZSM.

Diagnosis. In the Afrotropical realm, imagines of *U. nicholsae* most closely resemble those of *U. meruensis* (Fig. 7) and *U. delineatalis* (Fig. 1). They can be distinguished from those of *U. meruensis* by the fore- and hindwings concolorous, whereas in *U. meruensis* the hindwings are beige and much lighter than the dark brown forewings. *Udea nicholsae* can be distinguished from *U. delineatalis* by the evenly brown hind wings, whereas in *U. delineatalis* the hindwings are light beige in the basal area and brown in the area outside the postmedian line.

Description of adults. ***Head*:** Dorsal side brown, ventral side beige; labial palps porrect, in females more than twice as long as eye diameter, dorsal side brown, ventral side beige; maxillary palps well developed, long enough to touch each other at apex; haustellum fully developed, basally with beige scales; frons brown, evenly rounded; compound eyes large, hemispherical; antennae brown with swollen pedicellus, flagellum about 2/3 length of forewing, with very short ciliation; vertex in centre and behind ocelli with tuft of long brownish scales. ***Thorax*:** Dark brown dorsally, ochre-cream ventrally. Tegulae large, dark brown, with lighter brown tip. Legs ochre-cream, proximal foreleg tarsus with brownish scales. Outer tibial spurs half as long as inner spurs, respectively 2/3 length of inner spur in hindlegs' distal spur pair. ***Wings*:** (Fig. 6) Forewing length of females 9 mm. Number of frenulum bristles variable in females: holotype with three bristles on one side and two on other, paratype with two bristles on both sides. Forewings with ochre-brown ground

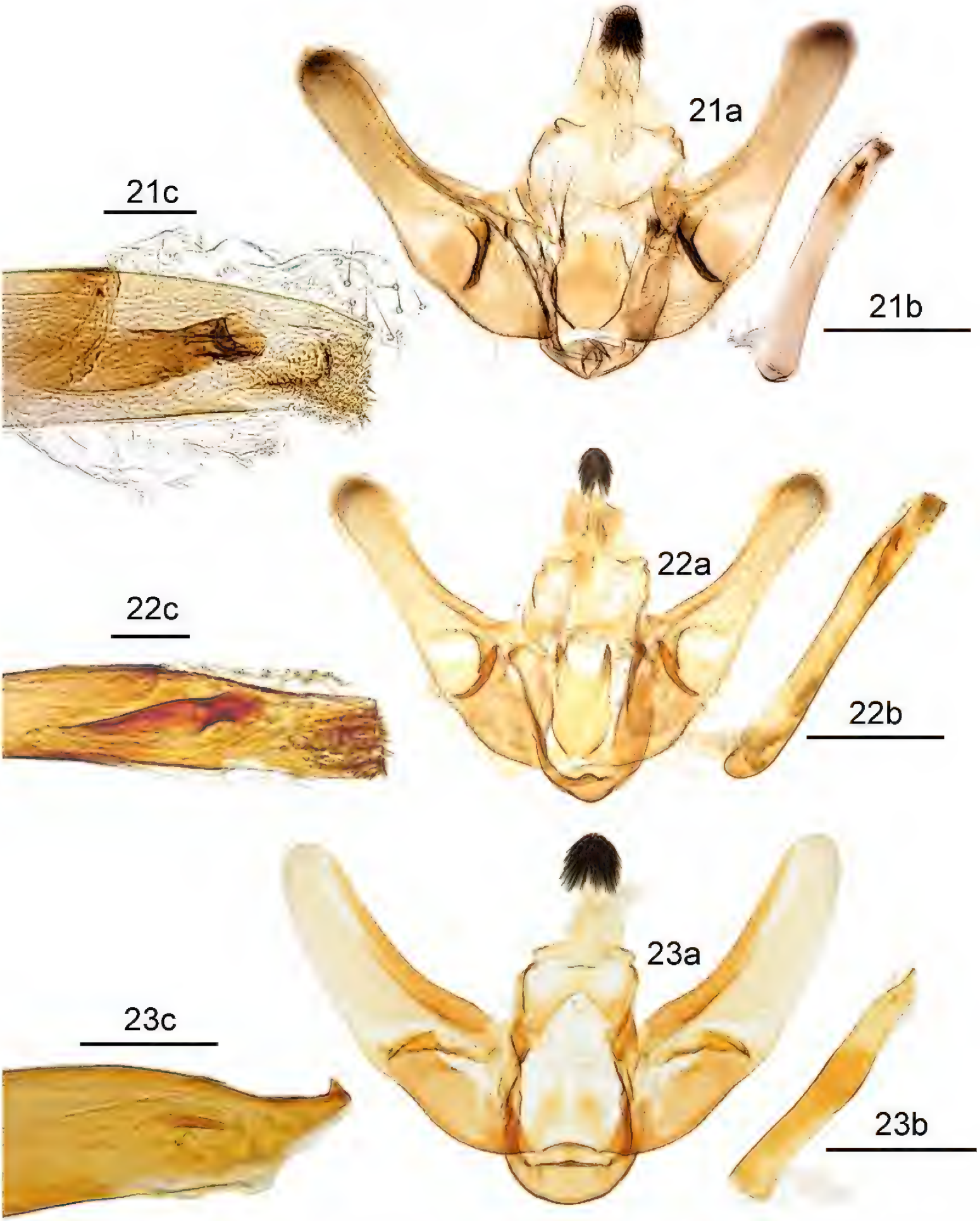
colour. Faint dark brown antemedian line leaving costa at 1/5 obliquely outward, at half its length abruptly directed straight towards anal margin, which it meets in a right angle. Discoidal stigmata with thin dark brown outline and slightly lighter brown filling, proximal stigma relatively large, oval, distal one larger, roughly 8-shaped. Postmedian line dark brown, leaving costa at 2/3 in a bow around distal discoidal stigma, behind stigma leading straight towards forewing base, then under stigma bending into a straight line towards anal margin, running in parallel to antemedian line. Veins on outer margin marked with dark brown dots, terminal wing margin with brown line. Fringe scales basally ochre, distal 2/3 brown. Underside pale brown ochre, distal costa with four dark brown spots, the second one being largest; very faint greyish proximal discoidal stigma, distal stigma more clear and larger, but blurry; faint postmedian line with course as in upper side; terminal dark brown dots on veins, terminal wing margin and fringe scales as in upper side. Hindwing ground colour slightly lighter than that of forewings, except for subterminal area. Dark brown spot-like proximal discoidal stigma slightly proximal of where forewings' antemedian line meets anal margin, distal discoidal stigma smaller, in hindwing centre. More or less faint postmedian line running from where forewings' postmedian line meets anal margin, running in a bow around distal discoidal stigma, fading out towards anal margin. Veins on outer margin marked with dark brown dots, terminal wing margin with brown line. Fringe scales ochre, those at vein dots brownish. Underside beige to ochre, discoidal stigmata dark brown, large; postmedian line mainly consisting of a sequence of dark dots: one large dot at costa, a pair of dots in curve outside distal discoidal stigma, a thin diffuse line leading to another pair of fainter dots in subanal area, and a final diffuse anal dot; terminal dark brown dots on veins, terminal wing margin and fringe scales as in upper side. ***Abdomen*:** Dark brown, interspersed with ochre scales. Tympanal organs (Fig. 16) with lobulus well developed, short, broad. ***Male genitalia*:** Unknown. ***Female genitalia*:** (Fig. 30) Papillae anales simple, with long chaetae. Apophyses posteriores slender, slightly curved dorsad; apophyses anteriores about 1.5-times as long as apophyses posteriores, thicker, widest at 1/4 length from the base, distal half slightly curved dorsad. Antrum simple, sclerotised, broadly funnel-shaped with posterior half with straight, roughly parallel sides and anterior half evenly narrowing to about 1/3 posterior antrum width. A short membranous section leads to colliculum; colliculum tubular, twice as long as broad, sclerotised except for a broad longitudinal membranous dorsal strip. Ductus bursae about as long as colliculum, slightly thinner. Ductus ejaculatorius attached at about 1/4 length of ductus bursae from colliculum. Corpus bursae large, ovate, membranous, anteriorly with minor longitudinal constriction, separating the corpus bursae into a shorter side and a longer one bearing the signum. Signum large, dentate, longitudinally oriented, broadest in anterior half of corpus bursae, anterior and posterior parts drawn out into long tapering arms, with posterior arm about twice as long as anterior one.

Distribution. So far only known from the type locality, Mount Meru in Tanzania.

Etymology. This species is named in honour of the late American actress Nichelle Nichols (December 28, 1932 – July 30, 2022), best known for her portrayal of communications officer Nyota Uhura on board the starship USS Enterprise in the science-fiction television series "Star Trek" as well as in six following feature films.

Genetic data. Not available.

Remarks. The species is placed in the *U. ferrugalis* species group (sensu Mally and Nuss 2011) based on the females exhibiting one of the two apomorphies for the group: the presence of a projection at the posterior end of the ductus bursae (folded over in fig. 30 and thus not observable there). The second apomorphy concerns male genitalia, which are not available for study at this time.



Figures 21–23. Male genitalia of *Udea* species, with male genitalia (**a**), phallus (**b**), and posterior phallus with cornutus (**c**). **21.** *U. delineatalis* (Walker in Melliss 1875); **22.** *U. ferrugalis* (Hübner, 1796); **23.** *U. hageni* Viette, 1852. Scale bars: 500 µm (**21a, b–23a, b**); 100 µm (**21c–23c**).

It is not unlikely that this species is endemic on the "mountain island" of Mount Meru, much like it appears to be the case for *U. momella* and *U. meruensis*, and for *U. kirinyaga* on Mount Kenya.

Udea meruensis Mally, sp. nov.

https://zoobank.org/E998A6DB-23D4-4E51-934A-760CF583BE26

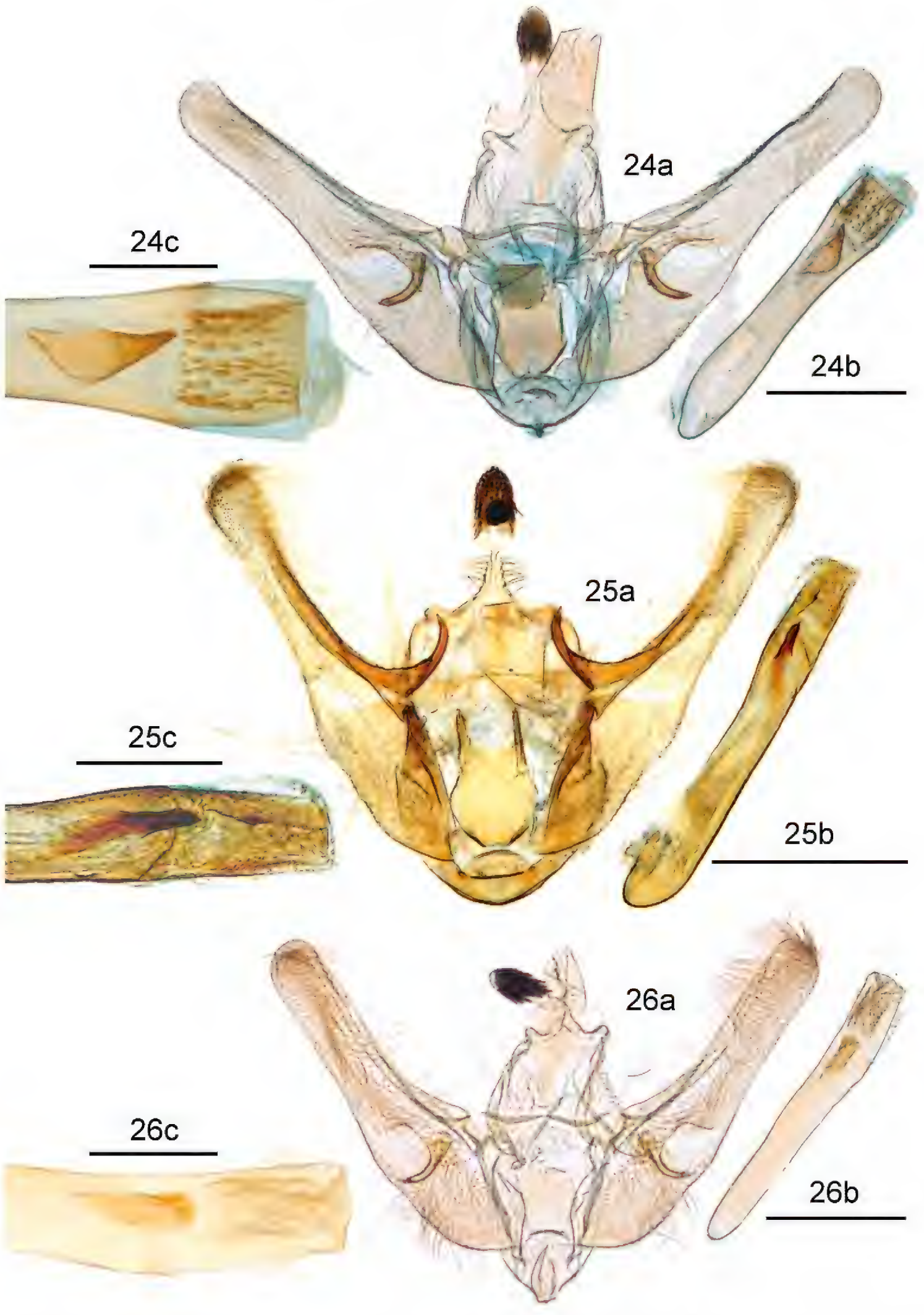
Figs 7, 17, 26

Type locality. Tanzania, Arumeru District, Mt. Meru Forest Reserve, 9km NNE of Olmotonyi, 2500 m, 3°15'57.5"S, 36°42'43.6"E.

Material examined. ***Holotype*:** Tanzania • 1 ♂; Arumeru District, Mount Meru Forest Reserve, 9 km NNE Olmotonyi; 3°15.9583'S, 36°42.7267'E; 2500 m a. S. L.; 8 Feb. 1992; L. Aarvik leg.; DNA voucher ZMBN Lep143; Mally genitalia dissection no. 951; unique specimen identifier NHMO 612836; NHMO. • ***Paratype*:** 1 ♂; same data as for holotype; Mally genitalia dissection no. 1189; unique specimen identifier NHMO 612837; NHMO.

Diagnosis. *Udea meruensis* is darker in forewing maculation than the other Afrotropical *Udea* species, although *U. delineatalis* (Fig. 4) is almost as dark, but its hindwings with a prominent distal discoidal stigma, a clear postmedian line and a distinct broad brown band from apex to tornus distinguish it from the new species. In the male genitalia, *U. meruensis* is distinguished from *U. kirinyaga* (Fig. 24) by the more V-shaped saccus, the shorter, more rounded juxta, and the stout, thumb-shaped main cornutus in the phallus. *Udea ferrugalis* (Fig. 22) is distinguished from *U. meruensis* (Fig. 26) by the larger juxta apically adorned on each side with a strongly sclerotised pointed projection. The species is distinguished from the Eurasian *U. accolalis* by the fibulae, which are shorter and more straight in *U. accolalis* (see e.g., Slamka 2013, pl. 21).

Description of adults. ***Head*:** Dorsally greyish-brown, ventrally beige, relatively flat compared to other *Udea* species; labial palps porrect, somewhat ascending, broadly triangular, extending forward more than one eye diameter, dorsal and outer side with banded light- and dark-brown scales, ventral and inner side as well as outer side's base of first meron and a narrow ventral area on second meron beige; maxillary palps well developed, long enough to touch each other at apex, base beige, remainder light and dark brown; haustellum fully developed, basally with beige scales; frons rectangular, flatly rounded, with mix of light and darker brown scales; compound eyes large, hemispherical; antennae ochre-brown, scapus short, pedicellus large, somewhat swollen, flagellum in male anteroventrally with short dense ciliation, and on opposite side with very sparse single chaetae as long as flagellum diameter; vertex in centre and behind ocelli with tuft of long brown scales and a collar of long, narrow spatula brown scales. ***Thorax*:** Prothorax, anterior mesothorax and base of tegulae brown, posterior mesothorax, metathorax, distal part of tegulae as well as legs lighter brown to beige, forelegs with front of femur brownish. Midleg with outer tibial spur half as long as inner one, hindlegs with outer spur about 2/3 length of inner in both spur pairs. ***Wings*:** (Fig. 7) Forewing length of male 10 mm. Forewings with brown ground colour. Faint greyish antemedian line leaving costa at 1/5 obliquely outward, after 1/3 abruptly directed straight towards anal margin. Discoidal stigmata dark brown, proximal one simple circular, distal one a short zigzag line. Postmedian line greyish-brown, leaving costa at 2/3 straight inwards towards distal end of distal discoidal stigma, then very faintly bending towards centre of wing until acute-angled tip below discoidal stigmata, then progressing distad and bending towards anal margin, which it meets approximately in line with distal discoidal stigma. Subterminal line a broad brown band evenly arching from subapex to subtornus; apex of costa with two brown markings, one in apex and one slightly more proximal on costa. Veins on outer margin marked with brown dots. Brownish fringe. Hindwing ground colour cream. Clear brown proximal discoidal



Figures 24–26. Male genitalia of *Udea* species, with male genitalia (**a**), phallus (**b**), and posterior phallus with cornutus (**c**). **24.** *U. kirinyaga* Mally, sp. nov.; **25.** *U. momella* Mally, sp. nov.; **26.** *U. meruensis* Mally, sp. nov. Scale bars: 500 µm (**24a, b–26a, b**); 200 µm (**24c–26c**).

stigma, indistinct distal discoidal stigma with a faint postmedian line connecting it to costa. Light brown outer margin, broad at apex, narrowing towards tornus. Outer margin and fringe as in forewing, with mark vein markings. Wings ventral sides as dorsal sides, but somewhat darker and maculation more contrasted, with area proximal of postmedian line dark brown versus lighter brown area distal of it, and subtornal area cream; postmedian line in hindwing continued below distal discoidal stigma as line of dark brown dots trailing off towards anal area. ***Abdomen*:** Brown like forewing ground colour, posterior end of segments with fringe of cream-coloured scales. Tympanal organs (Fig. 17) with lobulus well developed, more than twice as long as broad. ***Male genitalia*:** (Fig. 26) Ovate uncus head with stiff bifid, anteriad directed chaetae on dorsal surface, neck slender, elongate, base of uncus broadly attached to tegumen; tegumen roughly rectangular, ventrally somewhat widened; transtilla arms elongate triangular, dorsal margin folded over; V-shaped vinculum leading into a roundly V-shaped saccus with a median keel and a blunt ventral tip; juxta large, plate-like, roughly pentagonal, with a longitudinal membranous "notch" in ventral half; valvae long, elongate, slender, narrowest at ca. 2/3 of costa from costa base; costa straight, apex rounded, ventral valva margin straight in apical valva half, elongate sacculus slightly bulging out, ventral sacculus margin with broad triangular protuberance that is in close connection with fibula base; fibula emerging near costa base from a triangular base, forming a slender ventrad, fang-like structure bending towards distal sacculus, almost reaching ventral valva margin. Phallus slender, anterior end rounded, slightly widening towards posterior end; vesica with short, stout thumb-shaped cornutus with an obliquely cut base, and with a broad field of numerous tiny cornuti posteriad of cornutus (in uneverted vesica). ***Female genitalia*:** Unknown.

Distribution. So far only known from the type locality, Mount Meru in Tanzania.

Etymology. This species is named after Mount Meru, the type locality.

Genetic data. The DNA of the holotype was extracted and is stored as Lepidoptera DNA sample no. 143 in the DNA collection of the ZMBN. 633 base pairs of the mitochondrial *COI* gene (GenBank accession number ON206731) have been sequenced from that DNA sample to be included in the phylogenetic analysis. Due to the age of the type material at the time of description, the nuclear *wingless* gene was not successfully sequenced as the DNA is probably too fragmented to be sequenced with the conventional primers and Sanger sequencing. A search against the *COI* full database on BOLD resulted in the closest match of 96.3% similarity with an unidentified *Udea* specimen from W-Bulgaria (Sample ID BIOUG15079-B07), and the next-closest match of 96.24% with a specimen of *U. ferrugalis*.

Udea namaquana Karisch & Mally, sp. nov.

https://zoobank.org/201004EE-75BF-4833-A93A-CFB28C7056C3

Figs 8, 18, 27, 31

Type locality. South Africa, Northern Cape, Namaqua district, Hondeklipbaai, 30°21'S, 17°23'E.

Material examined. ***Holotype*: South Africa** • 1 ♂; Namaqualand, Hondeklipbaai, 8 km OSO Ort [ESE of village]; 30°21'S, 17°23'E; 05 Nov. 1993; T. Karisch leg.; Strauchvegetation [scrub vegetation], light catch with 160 W ML; Karisch genitalia dissection no. 3955; unique specimen identifier DEI Lepidoptera, # 300009; SDEI. • ***Paratypes*:** 1 ♀; same data as for holotype; Karisch genitalia dissection no. 3957; unique specimen identifier DEI Lepidoptera, # 300010; SDEI • 1 ♂; Namaqualand, Vanrhynsdorp, 7.5 km südöstl. Ort [SE of village], nördl. der Matsikammaberge [north of the Matzikama mountains]; 31°39'S, 18°47'E; 02 Nov. 1993; T. Karisch leg.; light catch with 160 W ML; MNVD.

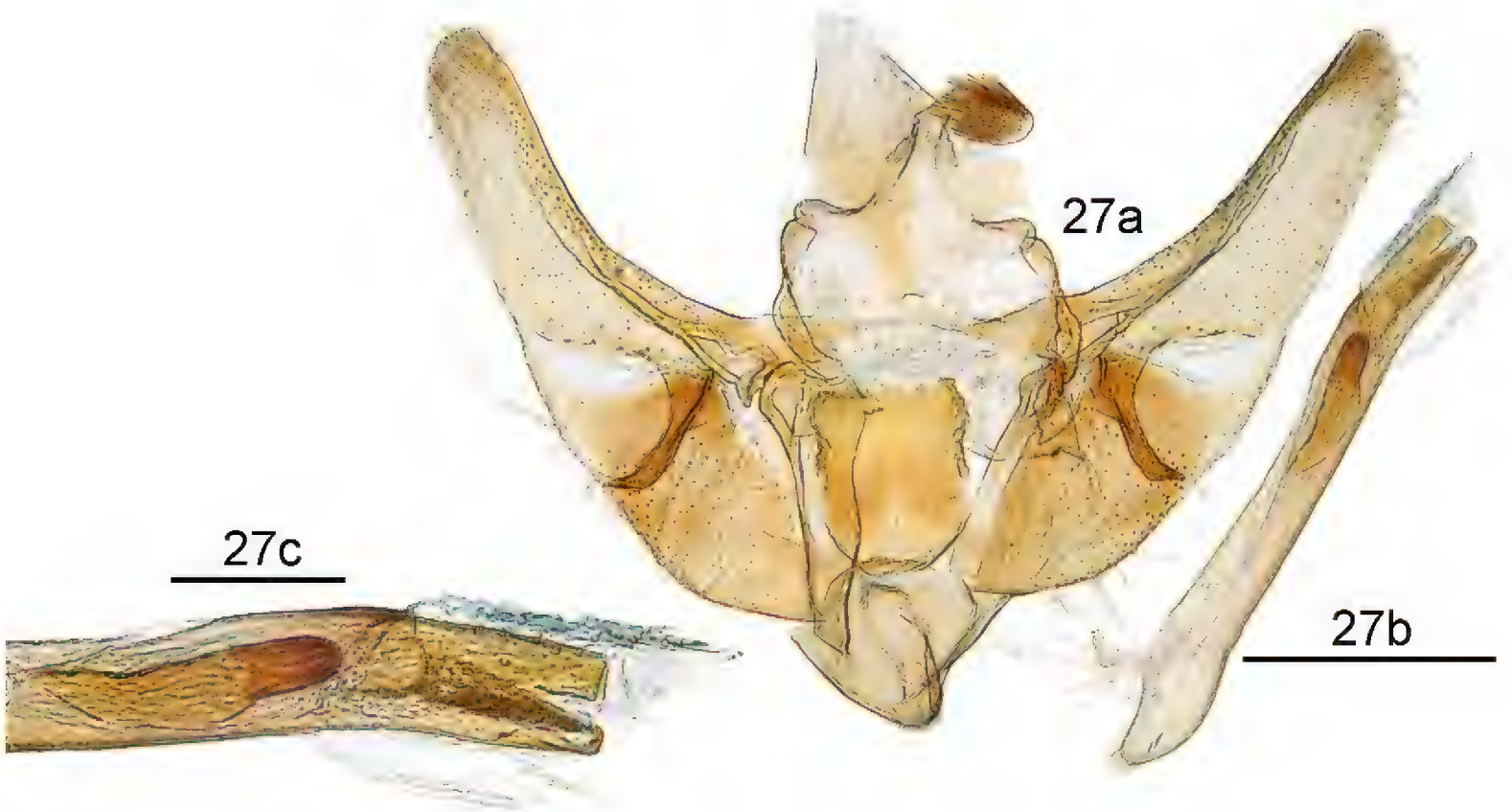


Figure 27. Male genitalia of *Udea U. namaquana* Karisch & Mally, sp. nov. Scale bar: 500 µm (**a, b**); 200 µm (**c**).

Diagnosis. Similar to *U. ferrugalis* (Fig. 2), but forewings more triangular, apex not as acute, ground colour more whitish, pattern distinct, grey marginal fascia of hindwing very faint or absent. In male genitalia the sacculus of *U. namaquana* (Fig. 27) is broader, the cucullus more triangular with an oblique tip, the juxta not bifurcate and without the numerous teeth on the projections, and the phallus a bit slenderer and more curved apically. The female of *U. namaquana* (Fig. 31) has a shorter but broader sterigma and a much narrower dentate signum ridge than in *U. ferrugalis* (Fig. 29).

Description of adults. ***Head*:** pale yellow, intermixed with yellowish-brown; labial palps about three times as long as eyes, 2nd segment broad covered with scales, ventral whitish, dorsal and lateral yellowish-brown, in female tip of scales brown whitish; maxillary palps ochre, slightly tinted grey, long enough to touch each other at apex; haustellum fully developed, basally with ivory-coloured scales; antenna filiform, shortly ciliate, flagellum yellowish-ochreous in male, at basal segments with some brown scales, yellowish in female. ***Thorax*:** pale yellowish, scales with a brown tip. Tibia of fore- and midlegs yellowish, tinged with brown, and yellowish on hindlegs. Outer tibial spur of mid-leg about 1/3 as long as inner, proximal spurs of hindleg with outer spur minute, about 1/10 as long as inner, distal spurs with outer spur about 2/3 as long as inner. ***Wings*:** (Fig. 8) Forewing length of males 8.5–9 mm, of female 9.5 mm. Forewings of pale-yellow ground colour, in male intermixed with brown. Antemedian line brown, indistinct from middle to dorsum in male, in female sharply angled. Proximal discoidal stigmata ellipsoid, distal discoidal stigmata narrow, lower part partly filled with brown scales. Postmedian line fine, greyish brown, slightly dentate, convex curved from costa to CuA1, with an abrupt dent inward at CuA2, but at this point only inner margin is visible, then continuing slightly dentate towards dorsum. Distal area along postmedian line and along margin less brown tinged in male. Black dots at veins on margin of the wings. Fringes yellowish white, some with brown tips. Underside whitish, pale yellow at costa, discoidal stigmata and postmedian line grey, the latter blackish at costa, between postmedian line and apex three minute black dots at costa. Hindwing

yellowish white, very slightly grey in apex. Discoidal spot faint, grey. Postmedian line grey, but very faint and only indicated at apex. Black dots at the margin of the wings at the veins. Fringes whitish, some with brown tips. Underside whitish, at costa more yellowish, inner and outer discoidal spot blackish or dark grey, postmedian line faint, grey, but starting with a blackish dot at costa. Marginal area at apex slightly greyish-brown. ***Abdomen*:** Pale yellowish. Tympanal organs (Fig. 18) with lobulus well developed, rounded to somewhat triangular, about as long as broad. ***Male genitalia*:** (Fig. 27) Uncus tip rounded, covered with stronger bristles, neck slender, broadened towards tegumen, with bulbous thickening at basis; tegumen roughly rectangular; Transtilla arms triangular, with long, tapered proximal ends; vinculum V-shaped, saccus quite broad, v-shaped; juxta large, plate-like, basal rounded, margin anterio-lateral stronger sclerotized and covered with some small teeth, upper margin frayed. Valva long, slender, cucullus (valva apex) gradually tapered, costa concave; fibula strong, with broad basis, bent at tip; sacculus broadest at middle. Phallus slender, slightly curved at distal ¼, with a strong cornutus, thimble-shaped at its tip, basis long; at tip of uneverted vesica a dense group of numerous small spines. ***Female genitalia*:** (Fig. 31) Papillae anales densely studded with long chaetae; apophyses posteriores thin, basally slightly bent, about half as long as apophyses anteriores; apophyses anteriores thin, more or less straight; antrum large, with a broad posterior opening tapering towards offset trapezoid anterior antrum section; colliculum slender, almost twice as long as broad, strongly sclerotised, with a broad longitudinal unsclerotised strip on ventral side; ductus bursae short, membranous, posteriorly with a small lateral protrusion; ductus seminalis small, membranous, attached at posteriormost ductus bursae, adjacent to colliculum; corpus bursae large, ovoid, membranous, partly with granulose surface structure; long lanceolate signum with numerous small teeth stretching through entire corpus bursae.

Distribution. So far only known from the Namaqualand in Western South Africa.

Etymology. This species is named after Namaqualand, an arid region in Namibia and South Africa, and the origin of the type material.

Genetic data. Not available.

Checklist of African *Udea* species

Udea Guenée in Duponchel 1845. Type species: *Pyralis ferrugalis* Hübner, 1796, by monotypy

= *Melanomecyna* Butler, 1883
= *Mnesictena* Meyrick, 1884
= *Notophytis* Meyrick, 1932
= *Protaulacistis* Meyrick, 1899
= *Protocolletis* Meyrick, 1888
= *Stantira* Walker, 1863

Udea delineatalis (Walker in Melliss 1875) (*Scopula*)

Udea ferrugalis (Hübner, 1796) (*Pyralis*)

= *ferruginalis* (Rossi, 1794) (misspell.)
= *feruginalis* Taylor, 1951 (misspell.)
= *Phlyctaenia epicoena* Meyrick, 1937 syn. nov.
= *Pionea granjalis* Chrétien, 1925

= *Pionea maculata* Costantini, 1923 (infrasubsp.)
= *Pionea obsoleta* Costantini, 1923
= *Scopula hypatialis* Walker, 1859
= *Scopula martialis* Guenée, 1854
= *Udea martialis* f. *fusca* Dufrane, 1960
= *Udea martialis* f. *pallida* Dufrane, 1960

***Udea hageni* Viette, 1952**

***Udea kirinyaga* Mally, sp. nov.**

***Udea meruensis* Mally, sp. nov.**

***Udea momella* Mally, sp. nov.**

***Udea namaquana* Karisch & Mally, sp. nov.**

***Udea nicholsae* Mally, sp. nov.**

Species removed from *Udea*

Achyra melanostictalis (Hampson in Poulton 1916) (*Pionea*) comb. nov.

Figs 9, 19, 32

Pionea melanostictalis Hampson in Poulton 1916: 175, pl. 2 fig. 46. Type locality: Somalia, Mandheera.

Material examined. ***Lectotype*** (here designated): Somalia • 1 ♀; Somaliland, Mandera, SW of Berbera; 914 m a. s. l.; 23 Sep. 1908; W. Feather leg.; "TYPE LEP: No 1212 Pionea 1/2 melanostictalis Hampson"; Mally genitalia dissection no. 1169; unique specimen identifier LEPI1212 1/2; OUMNH. • ***Paralectotype*:** 1 ♀; same data as for lectotype; 27 Sep. 1908; "TYPE LEP: No 1212 Pionea 2/2 melanostictalis Hampson"; unique specimen identifier LEPI1212 2/2; OUMNH.

Diagnosis. *Achyra melanostictalis* is readily distinguished from African *Udea* species by its wing pattern in combination with the dark, uniform hindwings lacking any stigmata. The species is preliminarily placed in *Achyra* based on commonalities in the wing pattern. It is distinguished from *A. coelatalis* (Walker, 1859) and *A. arida* Maes, 2005 by the clearly different wing pattern; see for example https://lepiforum.org/wiki/page/Achyra_coelatalis for *A. coelatalis*, and Maes (2005) for *A. arida*. With *A. nudalis* (Hübner, 1796), *A. melanostictalis* shares similarities in wing pattern, and in the female genitalia in the attachment location of the appendix bursae. However, the former species is distinguished from the latter in the female genitalia by two short ovate to lanceolate signa, and by the long, coiled ductus bursae. The two species share a rounded structure in the posterior female genitalia; in *A. melanostictalis*, however, this is the antrum, whereas in *A. nudalis* this structure is located in the posterior ductus bursae, before the colliculum and antrum. The species further resembles certain species of *Tegostoma* Zeller, 1847 (Odontiinae), like *T. comparalis* (Hübner, 1796) and *Tegostoma* sp. ABA4625 in the BOLD database, in wing shape, maculation and the uniformly coloured hindwings without maculation. *Achyra melanostictalis* can be best distinguished from *T. comparalis* in the female genitalia by the structure of the antrum, and the presence of an

appendix bursae as well as a signum (see e.g. Chen and Wang 2013 for illustrations of the female genitalia of *T. comparalis*). The unusual signum (Fig. 32) of *A. melanostictalis* is not shared with any other Spilomelinae, Pyraustinae or Odontiinae that we know of, and may therefore act as the most unambiguous character to identify and distinguish this species.

Description of adults. ***Head*:** Light brown; labial palps long, straight anteriad, basal meron cream-coloured, second and third merons brown; maxillary palps brown, long enough to touch each other at apex; haustellum well developed, with cream-coloured scaling at base; frons flat, brown with white lateral margins; complex eyes large, occupying the entire sides of head, hemispherical; ocelli present behind antenna base near compound eye; antennae cream-brown, with white ciliae almost as long as half antennomere diameter. ***Thorax*:** Dorsum dirty-greyish like wing colour, venter cream-white like basal meron of labial palps. Legs cream-white; midleg outer tibial spur about 2/3 length of inner spur; hindleg proximal pair with long inner spur and outer spur half as long, distal pair with outer spur 2/3 length of inner spur. ***Wings*:** (Fig. 9) Forewing length of females 7.5 mm. Female with two frenulum bristles. Forewing upper side light brown, costa darker brown; maculation dark brown, fairly clear; antemedial line narrow, from 1/4 of forewing length running in a zigzag line from below costa towards 1/3 of anal margin, in centre with a larger spike towards wing base, and basal of its tip a short streak; proximal discoidal stigma a small oval dot, distal discoidal stigma a short zigzag line spanning breadth of cell; postmedial line narrow, in costal third of its course with a wide amplitude, then fading and turning towards wing base under discoidal stigmata before becoming a more clear, broader line again that turn straight towards anal margin under discoidal stigmata; terminal area with a band of outward-directed brown spikes, retracing the zigzag pattern of postmedial line; termen with dark brown wedge-shaped markings alternating with terminal area's brown spikes; fringe basally narrowly light brown, followed by a narrow, slightly darker brown band, distal half pale brownish. Underside of forewings light brown, framed by slim dark brown costal margin and series of brown dots of termen at end of veins; anal margin with a broad beige area and only interspersed by brown scales; pattern of upper forewing diffusely mirrored on underside, with distal discoidal streak-like stigma being the clearest feature; fringe as on upper side. Hindwings on upper side uniformly brown, with colour as in forewing costa, veins being slightly darker brown; termen a dark brown line; fringe as in forewing. Underside of hindwings basally beige, centre light brown, darker towards termen; centre with a weak discoidal brownish streak; a weak brownish postmedial line stretching across anterior 2/3 of wing; fringe as on upper side. ***Abdomen*:** Dorsum brownish, with posterior edge of segments whitish, venter cream-white. Tympanal organ (Fig. 19) with bullae tympanicae almost spherical; fornix tympani recessed within tympanic frame; lobulus absent; venulae secundae strongly developed, slightly diverging posteriad. ***Male genitalia*:** Unknown. ***Female genitalia*:** (Fig. 32) Papillae anales membranous, densely studded with relatively short chaetae; apophyses posteriores more or less straight, strongly sclerotised, about as long as apophyses anteriores; apophyses anteriores week and rather short; antrum large, posterior part consisting of two large lateral plates (opened up dorsally in Fig. 32) meeting at a folded ventral recess, anterior part a large circular sclerotised structure; without discernible colliculum; ductus bursae short (about half as long as corpus bursae), relatively broad, membranous, somewhat widened in middle setion; ductus seminalis small, membranous, attached at posterior ductus bursae; corpus bursae large, ovoid, membranous; complex signum running obliquely through anterior corpus bursae: signum more than twice as long as broad, central section consisting of a narrow ridge, crossed at centre by transverse narrow ridge ending in slender lobes, apices of signum each consisting of a broad semi-circular to ovoid area

studded with spike-like teeth; membranous appendix bursae emerging from right side of posterior corpus bursae.

Distribution. So far only known from the type locality Mandheera (9°54.64'N, 44°42.79'E) in the southern Sahil region of Somaliland, Somalia.

Genetic data. Not available.

Remarks. The species is placed in *Achyra* based on a personal communication with Koen Maes, who suggested this genus based on the observation of African *Achyra* species with similar wing maculation (pers. comm. K. Maes 11/2021). Further arguments for this generic placement are the shape of the venulae secundae and the lateral attachment of the appendix bursae to the corpus bursae, both as in *A. arida* Maes, 2005. On the other hand, the female genitalia posterior of the corpus bursae, with the short, uncoiled ductus bursae and the large antrum, does not correspond to the general morphology of *Achyra*. The wing maculation of *A. melanostictalis* furthermore resembles some species of the Odontiinae genus *Tegostoma*, but the female genitalia share no resemblance. In fact, the signum in the corpus bursae is quite outstanding in its structure and to our knowledge unprecedented among Pyraustinae, adding to the difficulty of placing this species to genus. The appendix bursae attaching laterally to the corpus bursae is a feature of Pyraustini (character 114:0 in Mally et al. 2019). We hope that by illustrating the imago and the available genitalia here, someone might recognise its similarity to (and potential relationship with) another Afrotropical species. With the transfer of *A. melanostictalis*, *Achyra* now comprises 20 species, with four of them present in the Afrotropical region (Nuss et al. 2003–2022).

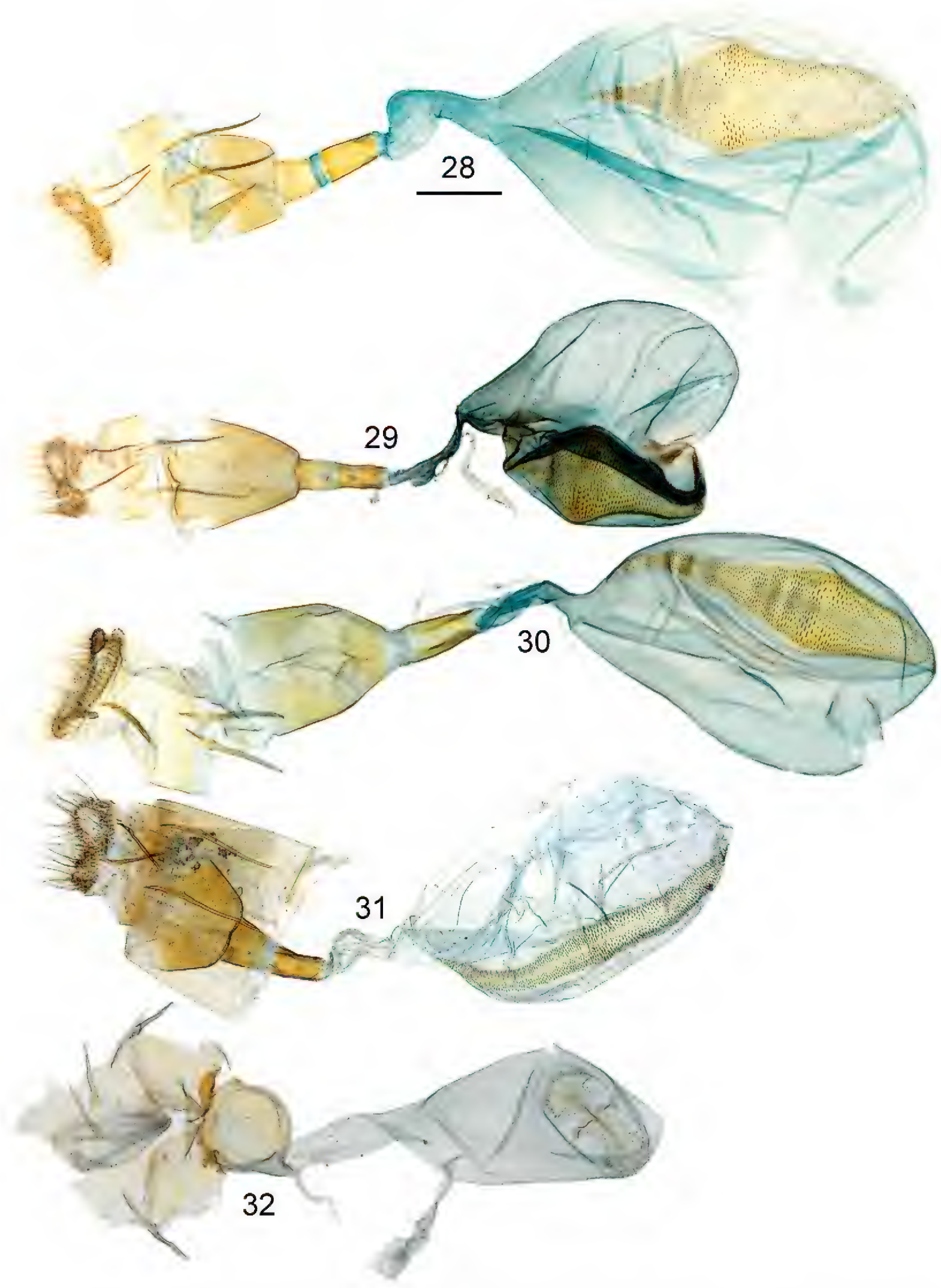
Lirabotys infuscalis (Zeller, 1852) comb. nov.

Figs 10, 20, 33–34

Botys infuscalis Zeller, 1852: 41–42. Type locality: South Africa, KwaZulu-Natal.

Material examined. ***Holotype***: South Africa • ♂; [handwritten] "*Botys* | *infusalis* [sic!]"; "Caffra- | ria."; [handwritten] "*196*"; [small blue rectangular label without text]; unique specimen identifier NHRS-TOBI000003347; NHRS. **Additional material:** South Africa • 1 ♂; Gauteng, Mogale's Gate Biodiversity Centre; 1420 m; 25°56.4667'S, 27°38.7833'E; 13 Feb. 2012; A. Hausmann leg.; DNA Barcode voucher [turquoise label] BC ZSM Lep 66598; ZSM • 1 ♂; same collection data as for preceding; 1500 m; 25°56.8667'S, 27°37.35'E; 14 Feb. 2012; DNA Barcode voucher [turquoise label] BC ZSM Lep 66756; Mally genitalia dissection no. 1067; ZSM • 2 ♀♀; same collection data as for preceding; 1660 m; 25°56.4667'S, 27°37.6'E; 16 Feb. 2012; Mally genitalia dissection no. 1066; Mally genitalia dissection no. 1068; ZSM.

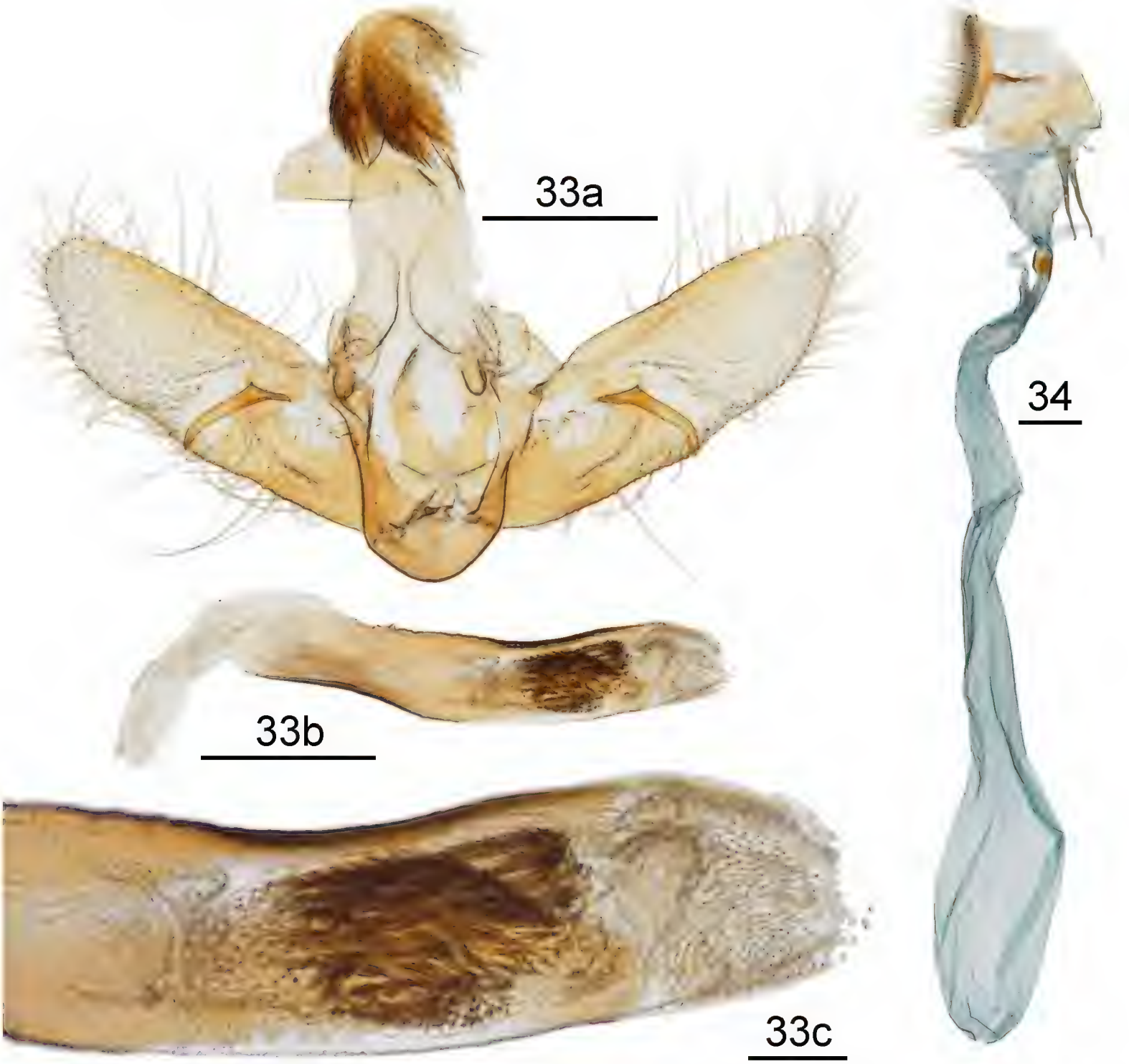
Diagnosis. Externally, *L. infuscalis* is easiest distinguished from Afrotropical *Udea* species by the long, slender forewings and the presence of a frenulum hook in the male's forewing. *Lirabotys infuscalis* (Fig. 10) differs from *L. liralis* (Legrand, 1966), the type species of *Lirabotys* Shaffer & Munroe, 2007, and from *L. prolausalis* (Walker, 1859) (see e.g. digitised holotype specimen of syn. *Botys longalis* Walker, 1866 at www.oum.ox.ac.uk/collections/irn/ca3358) in the wing maculation: *L. liralis* and *L. prolausalis* lack the proximal discoidal stigma, the distal discoidal stigma is a narrow arched line, and the postmedial line is traceable from costa to anal margin, and lacks the zigzag cource of *L. infuscalis*. It differs from *Lirabotys liralis* in the male genitalia (Fig. 33) in the shape of tegumen, sacculus, fibula, valva apex, and juxta, and in the size and number of phallus cornuti; in the female genitalia (Fig. 34) in the shape of the antrum, and the absence of a signum. The genitalia of *L. profusalis* (or its synonym *Botys longalis*) have not been studied.



Figures 28–32. Female genitalia of *Udea* species and species removed from *Udea*. **28.** *U. delineatalis*; **29.** *U. ferrugalis*; **30.** *U. nicholsae* Mally, sp. nov.; **31.** *U. namaquana* Karisch & Mally, sp. nov., including 7th abdominal segment; **32.** *Achyra melanostictalis*. Scale bar represents 500 µm, all figures to scale.

Description of adults. ***Head*:** Haustellum well developed, with cream-coloured scaling at base. Labial palps long, straight anteriad, basal meron and ventral side of second meron cream, rest sandy yellow; length of labial palps identical in both sexes. Maxillary palps well developed and long enough to touch each other at apex, sandy yellow. Frons rounded, sandy yellow to cream-coloured with white lateral margins, especially at antenna bases. Complex eyes large, hemispherical. Antennae cream, ciliae short, about 1/4 of antennomeres' diameter. Ocelli present behind antenna base near compound eye. ***Thorax*:** Dorsum sandy yellow to cream, venter and legs cream like basal meron of labial palps; midlegs with 1 pair of tibial spurs, hindleg with 2 pairs of tibial spurs. ***Wings*:** (Fig. 10) Forewing length 10.5–11.5 mm. Male and female with one frenulum bristle, in male fixed by a frenulum hook. Upper side of forewings orangish, veins in distal part somewhat darker; antemedial line not evident; discoidal stigmata brown, roundish dots, distal stigma about twice as large as proximal one; postmedial line somewhat darker than ground colour, emerging from 3/4 of forewing length, arching towards termen to about the level of discoidal stigmata, then running in a zigzag line towards area below distal discoidal stigma, then fading and not traceable anymore; termen a dashed line the colour of the postmedial line; fringe uniformly pale orangish-beige. Underside of forewings pale orangish, interspersed with brownish scales especially in apex and along costa; maculation matches that of upper side, but more contrasted, brown; termen with black dashed line, more prominent than in upper side; fringe as in upper side. Hindwings on upper side uniformly beige with an orangish hue, basal area darker orangish, veins and intervenal folds brownish, especially towards termen; a very vague postmedial line may be visible in the central part of its course; termen like in forewing but with shorter dashes; fringe like in forewing. Underside of hindwings uniformly beige, interspersed with brownish scales along costal and apico-terminal margins; proximal discoidal stigma as a rounded brown dot the size of the same stigma in the forewings' upper side; postmedial line more prominent then on upper side, consisting of a sparse line of brownish scales; termen with dashed line matching the pattern on the upper side, as prominent as in forewings' underside; fringe as in upper side.

***Abdomen*:** Dorsum sandy yellow like rest of upper side; venter cream like ventral thorax and basal meron of labial palps. Tympanal organs (Fig. 20) with ovate bullae tympani; fornix tympani projecting ventrad from tympanic frame; very short, broad lobulus; venulae secundae converging in a V-shape at about 80°. ***Male genitalia*:** (Fig. 33) Uncus head consisting of two sharply separated lateral lobes arching from a bulbous anterior part over uncus apex ventrad into a larger, oval part densely studded with stout bifid chaetae; tegumen long, slightly tapering from connection with vinculum towards uncus, ventral tegumen on each side with a short bullous ventrad protrusion; large oval transtilla arms sparsely studded with chaetae, and without any apparent connection of arms, no transtilla inferior sensu Marion (1954) present; vinculum somewhat rectangular, with a short U-shaped saccus; juxta large, elongate ovate, with a deep U-shaped central recession in its sclerotization, reaching from apex about 70% towards juxta base. Valvae elongate ovate; costa thin at base, widening in basal half of valva; costal margin straight to slightly concave; ventral valva margin with most of basal 2/3 straight, then concavely bending into straight distal 1/3 that leads into evenly rounded valva apex; sacculus large, stretching along basal 40% of ventral valva margin and across half the valva width, dorsal sacculus margin with broad central U-shaped recession in sacculus sclerotization, dorsodistal edge in close association with fibula base. Fibula emerging from oval base situated ventrally of thickened costa, fibula forming a slender, long claw-shaped structure directed ventrad towards distal sacculus end on ventral valva margin, slightly reaching over this



Figures 33–34. Genitalia of *Lirabotys infuscalis*. **33a.** male genitalia; **33b.** phallus; **33c.** posterior phallus with cornuti; **34.** female genital. Scale bars: 500 µm (**33a, b, 34**); 100 µm (**33c**).

margin. Phallus roughly cylindrical, slightly bent dorsad, apodeme evenly sclerotised, thinnest directly posterior of Ductus seminalis; no phallus coecum present. Vesica with large cluster of small needle-like cornute, posterior to these (in uneverted vesical) a granulose area of minute short teeth. ***Female genitalia*:** (Fig. 34) Papillae anales simple, with long chaetae. Apophyses posteriores slender, with a slight central angle bending distal half dorsad; apophyses anteriores about twice as long as apophyses posteriores, more or less straight, somewhat thicker, widest at 1/3 length from base. Antrum simple, membranous with a fine granulose texture, broadly funnel-shaped. Colliculum tubular, short, as long as broad, sclerotised except for a broad longitudinal membranous dorsal strip. Ductus bursae long, membranous, short posterior thin section between colliculum and ductus ejaculatorius somewhat wrinkled, ductus continuously broadening into corpus bursae without clear distinction between ductus and corpus bursae. Ductus ejaculatorius attached close to colliculum,

membranous. Corpus bursae large, ovate, membranous, without signum or any other sclerotisation. Appendix bursae absent.

Distribution. So far only known from South Africa, where it is recorded in the KwaZulu-Natal and Gauteng provinces (Zeller 1852; Hampson 1898).

Genetic data. DNA Barcode BIN BOLD:ABW0593. All COI sequences available on BOLD have the identical nucleotide sequence, and this sequence was used as consensus sequence for the phylogenetic analyses. In the BOLD identification tool, the DNA Barcode of *L. infuscalis* had the closest match with *Agrotera discinotata* Swinhoe, 1894, with a sequence similarity of 92.38% (after a pierid butterfly identified as *Moschoneura ela ela* with 92.83% similarity; the last sequence [MT787484] is packed with N's and should ideally be removed from the BOLD database as uninformative).

Remarks. The holotype of this species is also illustrated on the website of the NHRS (http://www2.nrm.se/en/lep_nrm/i/botys_infuscalis.html). We place this species in *Lirabotys* based on several similarities between *Botys infuscalis* and *Lirabotys liralis* (Legrand, 1966), the generic type species (see Shaffer and Munroe 2007): both share a similar wing shape and maculation, the male bears a frenulum hook, and in the male genitalia, the uncus head consists of two lateral lobes densely studded with chaetae, the valvae have a similar elongate shape, and the slender, long fibulae emerge from the same area on the valva. However, there are also differences between the two species: in the male genitalia, the tegumen is of a different structure, the juxta differs in shape (small and lanceolate in *L. liralis*), as does the sacculus, and the phallus bears multiple needle-like cornuti (versus a single "spine-like cornutus about half length of [phallus]" in *L. liralis* (Shaffer and Munroe 2007); the female genitalia lack the lateral projections of the antrum and the strong four-armed signum of *L. liralis*.

The fornix tympani of the tympanal organ is projecting ventrad from the tympanic frame, a unique synapomorphy of Spilomelinae (characters 22:0 and 23:0 in Mally et al. 2019). This observation challenges the placement of *Lirabotys* in Pyraustinae, or the treatment of this character as synapomorphy of Spilomelinae – a contradiction that demands further research.

With the transfer of *L. infuscalis*, *Lirabotys* now comprises six species, all Afrotropical in distribution (Nuss et al. 2003–2022).

Genetic & phylogenetic results

After 2,000,000 generations, all minimal Estimated Sample Sizes (ESS) were ≥ 388, indicating that all parameters have been well sampled; the Potential Scale Reduction Factor (PSRF) reached 1.000 for all but two parameters with 1.001. These values were deemed sufficient for the Bayesian inference. In the Bayesian tree (Fig. 36), the three included Pyraustinae group together at the base of the tree. *Udeoides* (represented by two species) is sister to a clade comprising the monophyletic *Udea* and their sister group, *Deana hybreasalis* + *Mnesictena marmarina*. Within *Udea*, the largely polytomic *U. ferrugalis* group is sister to the remainder of *Udea*, which comprises the *U. itysalis* group + (*U. alpinalis* group + (*U. prunalis* group + *U. numeralis* group)). In contrast to the results of Mally and Nuss (2011), we find *U. rhododendronalis* not as sister to the *U. prunalis* group, but sister to the *U. alpinalis* group instead; however, as in the results of Mally and Nuss (2011), this relationship is very poorly supported.

Considerable branch support is only found for a few larger groups: *Udeoides* (0.98 PP), the *U. itysalis* group (1.0 PP), their sister group (0.97 PP) and the clade comprising these two (0.95 PP).

With the extended morphological character matrix (Tab. 2), a third synapomorphy is recognised for the *U. ferrugalis* group: 17:1, orientation of fibula base towards sacculus centre or base.

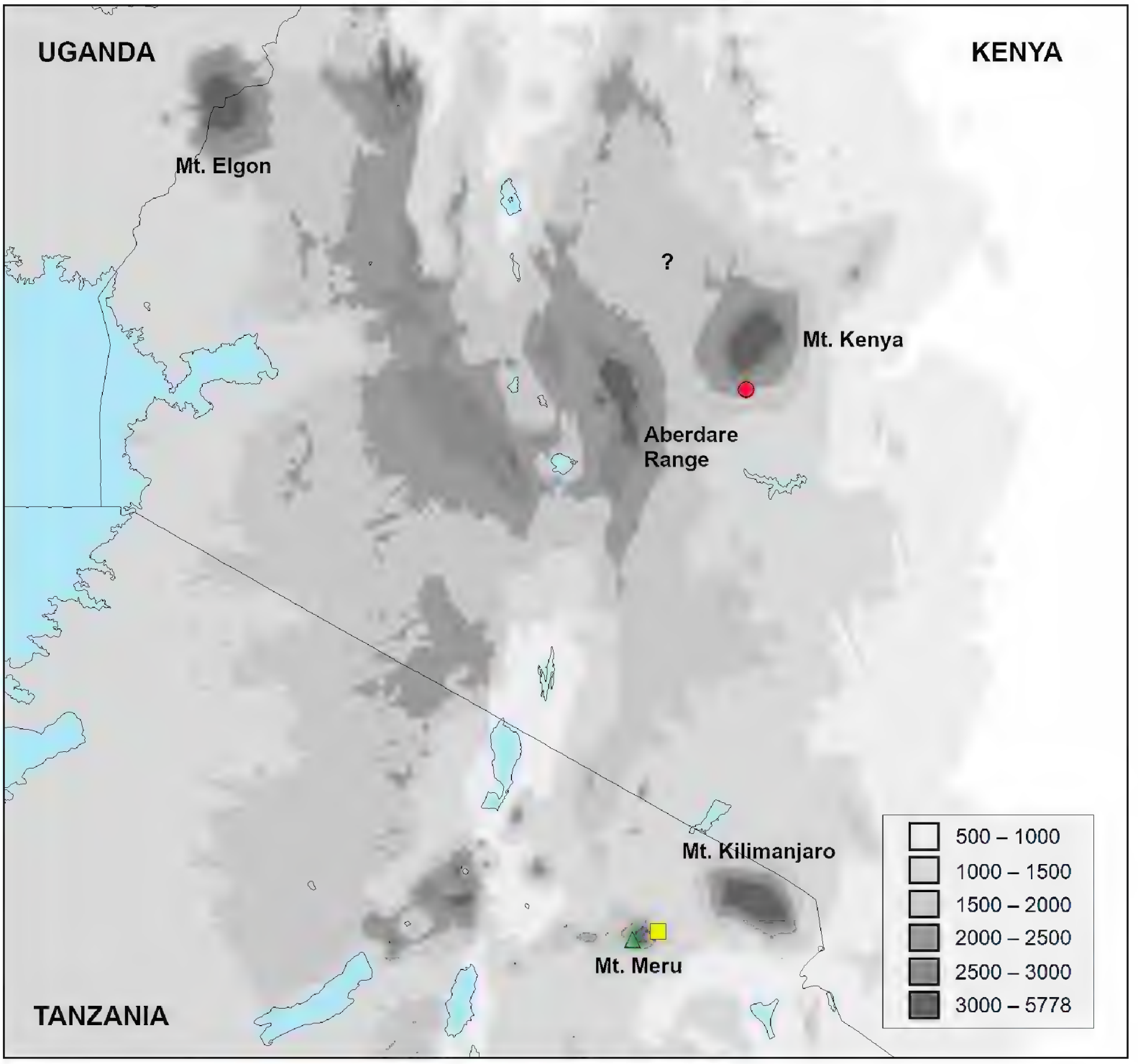


Figure 35. Elevation map of the southern part of the Gregory Rift with the collection sites of *Udea kirinyaga* (red dot) at Mount Kenya, and *U. meruensis* (green triangle) as well as *U. nicholsae* and *U. momella* (yellow square; same collection site) at Mount Meru; the "?" represents the collection site of a DNA-barcoded specimen that might represent an additional species (see section "Genetic data" under *U. ferrugalis*); elevations ≥ 500 m are marked in increasingly darker grey shades every 500 m.

Discussion

The phylogenetic results place the five *Udea* species described as new in the present study in the *U. ferrugalis* species group sensu Mally and Nuss (2011). This is in accordance with the synapomorphies proposed by that study for the *U. ferrugalis* group: a cluster of small cornuti on the vesica (present in *U. kirinyaga*, *U. momella*, *U. meruensis* and *U. namaquana*), and a projection at the posterior end of the ductus bursae (present in *U. nicholsae* and *U. namaquana*). The poor data coverage (26 coded morphological characters versus 50 taxa; Tab. 2) for some of the investigated taxa resulted in polytomies, especially in the *U. ferrugalis* group and less so in the *U. numeralis* group (Fig. 36).

The two newly added morphological characters add synapomorphies to the phylogeny of *Udea*: the fibula base oriented towards the sacculus centre or base (17:1) is a synapomorphy for the *U. ferrugalis* group, while in the remainder of *Udea* and the *Udea* sister groups the fibula base points towards the distal sacculus end (17:0). The sacculus being broadest distad of fibula base (18:0) is a synapomorphy for the clade comprising the *U. alpinalis* group + (*U. prunalis* group + *U. numeralis* group); all taxa basal of this clade have the sacculus broadest basad of or at the fibula base (18:1).

Udea kirinyage, *U. meruensis*, *U. momella* and *U. nicholsae* appear to be species of high elevations, and to our current knowledge they are endemic to the "mountain islands" of Mount Kenya and Mount Meru, respectively (Fig. 35). It is reasonable to assume that additional endemic *Udea* species are present in other parts of the West African mountain ranges, like the Kenyan Aberdare Range, Mau Escarpment and Cherang'any Hills, Mount Elgon on the border to Uganda, and Mount Kilimanjaro, the Crater Highlands and Mount Hanang in Tanzania.

Many species that have been associated with the *U. ferrugalis* group are endemic on oceanic islands, like *U. delineatalis* on St. Helena, *U. maderensis* on Madeira, *U. nordmani* on the Canary Islands, *U. azorensis* on the Azores, and the species-rich Hawaiian *Udea* complex (see Zimmerman 1958). The two *Udea* species of the Galápagos Islands, *U. galapagensis* Landry, 2016 and *U. sideralis* Landry, 2016 (Landry 2016), do not appear to belong to this species group, as they share none of the group's synapomorphies. There are, however, also a considerable number of continental, often widespread species in the *U. ferrugalis* group, e.g. the North American *U. rubigalis* and *U. profundalis*, the Eurasian *U. ferrugalis* and *U. accolalis*, and the Asian *U. renalis* and *U. testacea*. DNA Barcode data investigated in our study indicates that the distribution range of *U. testacea*, described from Yokohama, Japan, also includes the Chinese mainland (Nankai) and stretches as far as Northern Pakistan (Khyber Pakhtunkhwa; see "Genetic data" under *U. ferrugalis*). Furthermore, the algorithm applied by BOLD (Ratnasingham and Hebert 2013) to place DNA Barcodes into BINs that match species appears to fail in distinguishing between *U. ferrugalis*, *U. delineatalis* and *U. testacea*, as they are all placed in the same BIN. Additional DNA Barcodes for the (poorly sampled) last two species, and/or an adjustment of the BOLD BIN clustering algorithm may aid in this issue.

Little is still known about the immature stages and biologies of the *Udea ferrugalis* group, and about *Udea* species in general. Whereas continental species like *U. ferrugalis*, *U. profundalis* (Packard, 1873) and *U. rubigalis* (Guenée, 1854) are markedly polyphagous on a large number of plants (Weigel et al. 1925; Robinson et al. 2010), species of the diverse Hawaiian group are confined to plants of one or two plant families (Zimmerman 1958). Island floras and faunas often harbour only a non-random subsample of those of the nearest larger landmass, a phenomenon known as "island disharmony" (König et al. 2020). Populations of insects establishing on islands thus face a limited spectrum of available foodplants. Pronounced polyphagy may be a very useful trait of such newly establishing populations, as it increases their chances of finding at least one suitable hostplant. This may at least in part explain why the *U. ferrugalis* species group, comprising several polyphagous species in the Nearctic and Palaearctic, is so well-represented in oceanic island faunas. It remains to be discovered whether the oceanic island endemics (and potentially also the mountain endemics) among the African *Udea* species exhibit a similarly narrow larval food spectrum as the Hawaiian species.

The phylogenetic results indicate that *U. hageni*, inhabiting the oceanic island of Tristan da Cunha, is not part of the *U. ferrugalis* group. The males lack the area of granulose cornuti on the vesica and the single large cornutus of the phallus. Instead, *U. hageni* is found to belong to

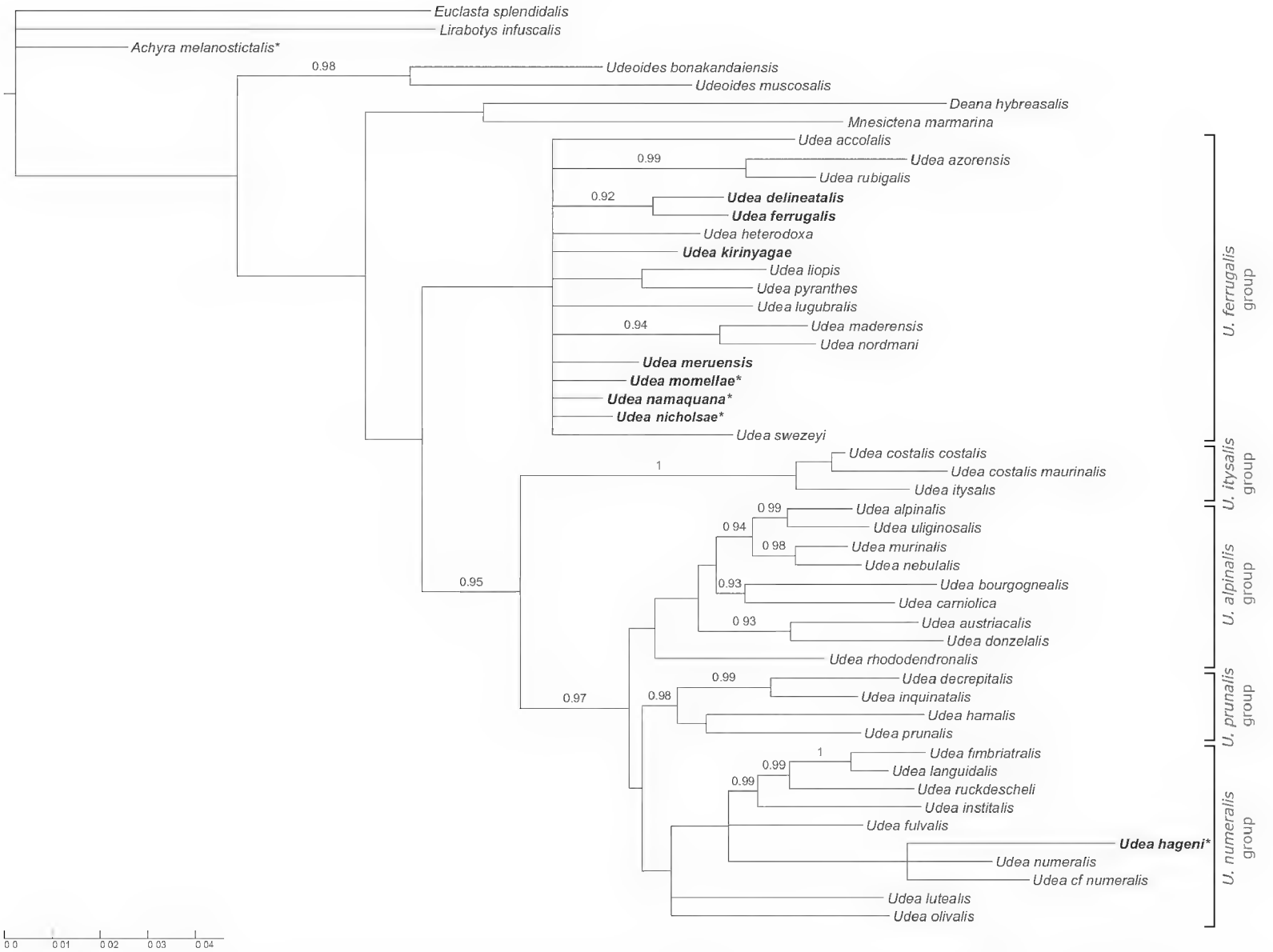


Figure 36. Bayesian phylogenetic inference tree of *Udea*, based on genetic and morphological data. Numbers on the branches represent posterior probabilities (PP) ≥ 0.9, scale bar represents substitutions per site; note that for the taxa marked with an asterisk (*), the analysis was done with morphological data only. The sampled African *Udea* species are marked in bold, *Udea* species groups sensu Mally and Nuss (2011) are indicated on the right.

the *U. numeralis* group, as sister to *U. numeralis* and *U.* cf. *numeralis* (Fig. 36). To our current knowledge, *U. hageni*, together with the two *Udea* species endemic to the Galápagos islands, are the only *Udea* species on an oceanic island that are not part of the *U. ferrugalis* lineage.

Udea rhododendronalis (Duponchel, 1834), a European species, is found as sister to the *U. alpinalis* group, with which it shares the sexual wing dimorphism. This relationship is not supported by branch support (posterior probability) though, as was the case in Mally and Nuss (2011), where the species was sister to the *U. prunalis* group. The inclusion of the morphologically very similar North American *U. vacunalis* (Grote, 1881) in a future phylogenetic analysis may provide further clarification for the relationship of *U. rhododendronalis*.

In comparison with other biogeographic regions, the Afrotropical region has the lowest number of *Udea* species (now 8 spp.), compared to 17 spp. in the Oriental region, 25 spp. in the Nearctic, 43 spp. in Austral-Asia (with 41 of these endemic to Hawaii), 49 spp. in each the East Palaearctic and the Neotropics, and 51 spp. in the West Palaearctic (Nuss et al. 2003–2022). Our results indicate that the Afrotropical region is dominated by representatives of the *U. ferrugalis* group, whereas the adjacent West Palaearctic region has a more mixed composition of *Udea* species groups, with the montane *U. alpinalis* group, the largely Mediterranean and Middle Eastern *U. numeralis* group,

the predominantly Nordic *U. prunalis* group, the *U. ferrugalis* group with three species on oceanic islands, and the *U. itysalis* group. This poor representation of *Udea* in Africa may change with the future discovery of additional species.

The ventrally protruding fornix tympani of *Lirabotys infuscalis* contradicts its placement in the Pyraustinae sensu Mally et al. (2019). A phylogenetic study should investigate the evolutionary relationships of this species to *Lirabotys* as well as other Pyraustinae and Spilomelinae.

Conclusions

This revision revealed that two of the six Afrotropical *Udea* species were misplaced in this genus, and that two other species – *U. ferrugalis* and *U. epicoena* – were referring to the same species. This resulted in only one continental species (*U. ferrugalis*) and two island endemics (*U. delineatalis*, *U. hageni*) in the Afrotropical realm. We furthermore discovered five additional species, with four of them presumably restricted to higher elevations of mountains in the East African Rift Valley system, bringing the currently known number of Afrotropical *Udea* species to eight. The descriptions of the new species are all based on a single or a few available specimens. Careful screening of collection material from the Afrotropics as well as targeted collecting in and around the type localities may reveal further material of these and other undescribed *Udea* species as well as specimens of immature life stages.

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